Frugivorous mutualisms in a native New Zealand forest; the good the bad and the ugly

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A thesis submitted in partial fulfilment of the requirements for the degree

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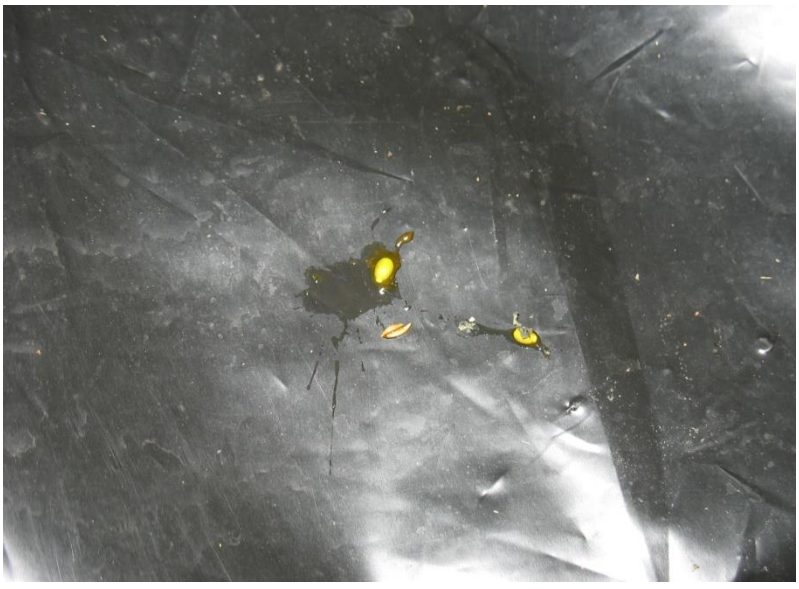
The good, large male bellbird (R/M-R/W) mist netted at Kowhai Bush

The bad, a large barberry plant prior to fruit removal



And the ugly, faecal samples of *Coprosma robusta* and *Ileostylus micranthus* seeds

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Abstract

Widespread anthropogenic invasions have prompted concerns that naturalized organisms could threaten biodiversity. In particular, invasive weeds can negatively affect native biota through a variety of means, including disrupting mutualisms. This thesis was designed to observe and test dispersal mutualisms in a native forest during autumn when the majority of plant species are fruiting.

In this thesis I examined whether the invasive plant barberry (*Berberis glaucocarpa*) was influencing the behaviour of a native frugivore bellbird (*Anthornis melanura*) and a range of dispersal related services in a native forest, Kowhai Bush near Kaikoura. To test these 18 banded bellbirds were followed through autumn 2011. These observe bellbirds were split between control and test bird. Barberry fruit was removed from the test bird territories. I recorded whether bellbirds changed their territory sizes, foraging and daily behaviours. During 52 hours of observations, bellbirds were never observed feeding on barberry fruit. No significant changes to bellbird behaviour or territories were observed after the removal of barberry fruit. Bellbird diet overall was dominated by invertebrates (83% of foraging observations), with smaller contributions from fruit (16%, nearly all on *Coprosma robusta*), nectar and honeydew. Since bellbirds did not eat barberry fruit, removal of this weed is unlikely to negatively affect bellbirds during autumn.

Which other bird species were dispersing barberry was recorded. I recorded 242 hours of videotape footage on 24 fruiting plants. A total of 101 foraging events were recorded of 4 different bird species: silvereyes (*Zosterops lateralis*) 42 visits, blackbirds (*Turdus merula*) 27 visits, song thrush (*Turdus philomelos*) 29, and starlings (*Sturnus vulgaris*) 3 visits. The species differed in the mean length of time they spent in plants, so the overall contribution to barberry fruit removal was 32.6% silvereyes, 24.3% blackbirds, 42.9% song thrush and 0.1% starlings.

To find out the relative contribution of exotic and native birds to dispersal of fruits in Kowhai Bush, I mist-netted 221 birds of 10 species and identified any seeds in the 183 faeces they deposited. A total of 21 plant species were observed fruiting in Kowhai Bush during this time. A total of 11 different plant species were identified from 1092 seeds. Birds were further observed feeding on 3 other plant species which were not observed in faecal samples. This left 7 plants with unobserved dispersal vectors. There were likely four main dispersers, bellbirds, silvereyes, song thrush and blackbirds and five minor, brown creeper (*Mohoua novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*), fantails (*Rhipidura fuliginosa*), dunnock (*Prunella modularis*) and starlings. However there was considerable variability between these bird species dispersal abilities. Introduced birds' song thrush and blackbirds were observed dispersing naturalized plant seeds at higher than expected rates in comparison to native frugivores bellbirds and silvereyes. I also measured the gape sizes on mist netted birds and on samples of fruit from Kowhai Bush. Both silvereyes and bellbirds were found to be eating fruit larger than their gape, but despite this two native (*Hedycarya arborea* and *Ripogonum scandens*) and three exotic plants (*Vitis vinifera, Taxus baccata* and *Crataegus monogyna*) had large fruit that were probably mainly dispersed by song thrush and blackbirds. Hence, introduced birds were important seed dispersers for large fleshy fruited seeds in Kowhai Bush. Demonstrating that interactions among native and exotic flesh fruited plants and frugivores is important within forest communities.

Chapter one
General Introduction

1.1 Seed dispersal

Seed dispersal is an exceptionally important mechanism for plants, as their limited mobility means they must rely on a variety of dispersal vectors to transport their seeds over distances (Bakker et al., 1996). In contrast to the sedentary nature of adults, seed dispersal often represents the only mobile stage in the life history of many plant species (Bakker et al., 1996). There are several reasons why seed dispersal is thought to benefit a plant. The first is to escape from the parent, which implies disproportionate success for seeds that can move away from the vicinity of the parent, as compared with those that fall nearby and must compete with their parent or siblings. Second, dispersal can facilitate colonization where parents produce offspring capable of taking advantage of vacant habitats which become open. Third, adult plants can obtain benefits from directed dispersal, in which diaspores reach localized sites suitable for establishment (Howe and Smallwood, 1982, Nathan and Muller-Landau, 2000, Willson and Traveset, 2000, Bakker et al., 1996). Thus, dispersal of propagules away from parental plants can increase the overall fitness of individuals in the parental population by increasing the likelihood of seed survival and the establishment of new populations (Bakker et al., 1996, Howe and Smallwood, 1982, Nathan and Muller-Landau, 2000, Willson and Traveset, 2000).

Patterns of seed dispersal are determined in large part by the dispersal mechanisms they use. This in turn is important for the demographic and genetic structure of plant populations (Howe and Smallwood, 1982). Furthermore, the establishment of new populations from seed dispersal helps sustain ecological integrity by redistributing the offspring of plants (Schupp, 1993, Schupp and Fuentes, 1995, Harms et al., 2000, Levey et al., 2002). Plants use a variety of dispersal mechanisms; these include both abiotic and biotic dispersal vectors. Howe and Smallwood (1982) reviewed several modes of seed dispersal used by plants: 1) gravity, in which the ripe seed simply falls from the tree, and in some instances the seed might then be dispersed later by another vector such as water or animals; 2) wind, in which the seeds have morphological

adaptations such as disk-like wings or plumes that are used to catch the wind and disperse the seed over long distances; 3) water, in which the seeds can travel for long distances in water currents, including over intercontinental distances which some palm trees seeds achieve; 4) ballistic dispersal, plants use their own ability to move seeds by firing them away from the adult plant; and 5) zoochory, animals are used to disperse plant seeds. There are in two main forms of zoochory: epizoochory and endozoochory. Epizoochory seed dispersal is the transport of seeds on the outside of the animals via a variety of seed adaptations including adhesive mucus, or a variety of hooks, spines and barbs (Sorensen, 1986). Endozoochory is the internal ingestion of seeds by vertebrates which, at a later stage, regurgitate or excrete the seeds (D'Hondt et al., 2012). One form of endozoochory which is exceptionally important in the dispersal of many plants is frugivory. This involves a plant surrounds its seeds with a reward, usually an edible and nutritious pulp, forming a propagule which is ingested by a dispersal vector, and then regurgitated or excreted later (Pijl, 1969, Ridley, 1930).

1.2 The importance of frugivorous seed dispersal mutualisms

Frugivory is an important mutualistic service on which many plant and disperser species depend (Thompson and Willson, 1979, Howe, 1977, Snow, 1971). The exact percentage of plant species that use frugivory as a form of dispersal is unknown. However, the percentage of fruiting species can vary widely between and within terrestrial ecozones (Howe and Smallwood, 1982). For example, in tropical rainforests at least 50 % and sometimes upwards of 75 % of tree species produced fleshy fruits dispersed by vertebrates (Howe and Smallwood, 1982). In temperate forests, the proportion of plants dispersed by vertebrates can be upwards of 60 % (Howe and Smallwood, 1982). Although most islands have high numbers of fleshy fruits in comparison to continental land masses, New Zealand does not appear to conform to this expectation (Lord, 1999). The frequency of species with fleshy fruits in New Zealand is not high when compared with other temperate floras (Lord, 1999). Approximately 25 % of New Zealand's indigenous plant genera and between 12-13.5 %, of its species produce fleshy fruit (Lord et al., 2002, Thorsen et al., 2009). However, fleshy-fruited species are more common than expected in alpine grassland communities (12%) and among tree species (70%) in New Zealand (Lord, 1999, Clout and Hay, 1989)

Vertebrates are the primary seed dispersal vectors for most fruiting plants (Bakker et al., 1996). However, some invertebrates such as ants can also be important seed dispersal vectors (Howe and Smallwood, 1982). For example, harvester ants (*Vermessor pergandei* and *Pogonomyrmex californicus*) can be important seed dispersers of *Datura discolor* seeds, which they carry to nests where they remove food bodies off the fruit and then discard the seeds underground (Howe and Smallwood, 1982)**.**

Fruit-disperser mutualisms involve reciprocal benefits, and many animal species depend on fleshy fruits as a food resources (Jordano et al., 2011). Much of the flesh surrounding seeds is a store of nutrients and thus the propagule represents a nutritional reward for any animal that consumes the fruit (Ruxton and Schaefer, 2012). The relative abundance of fruit, the short search times needed to obtain it, and in some areas, the year-long availability makes fruit an attractive food source (Morton, 1973). Because energy in many fruits is mainly in the form of simple sugars, the digestive processes used to gain direct energy are often easier than in more complicated foodstuffs such as plant foliage (Bairlein, 2002). In addition to sugars, many fruits contain lipids and proteins, making them an important source of energy and fat (Bairlein, 2002, Stiles, 1993). In some instances, fruit availability is so important that some species only breed when sufficient fruit is available to raise offspring e.g., kakapo, *Strigops habroptilus*; (Powlesland et al., 1992, Elliott et al., 2001). This mutualistic bond has had profound effects on seed dispersers and the evolution of frugivory. This in turn has contributed to large-scale biodiversity patterns through the evolutionary diversification of several clades of frugivorous primates, bats, fishes, reptiles and birds (Fleming, 2005, Fleming et al., 1987).

1.2.1 Historic and present frugivory in New Zealand

Globally, birds play an important role as seed dispersal vectors (Clout and Hay, 1989, Levey et al., 2002, Bakker et al., 1996). This relationship between plants and birds is exceptionally important (Morton, 1973). In New Zealand, birds historically and presently perform the vast majority of fruit dispersal services (Thorsen et al., 2009, Thorsen et al., 2011, Lee et al., 1991, Clout and Hay, 1989, Webb and Simpson, 2001). Over half (55 %) of New Zealand's terrestrial verterbrate fauna included fruit in their diet at least some of the time (Thorsen et al., 2011). However, despite this wide extent of frugivory, only a few species (6%) are considered to include fruit as a

major component of their diet and thus to be important at an ecological and evolutionary scale in the dispersal of seeds (Thorsen et al., 2011).

Due to human colonisation and the introductions of invasive animals over the past 1000 years, a large number of these native dispersal vectors have become extinct or declined in numbers (Thorsen et al., 2011, McGlone, 1989, Holdaway, 1999, Clout and Lowe, 2000). It is estimated that 57% of flighted and 80% of flightless frugivorous vertebrate species have became extinct since humans arrived in New Zealand (Thorsen et al., 2011). Furthermore, many native bird species populations have suffered regional population declines or extinctions due to predation or habitat loss (O'Donnell, 1996, Atkinson, 1973, Diamond and Veitch, 1981, Heather and Robertson, 1998, Clout and Hay, 1989).

It is now likely that plant-bird mutualisms in New Zealand are largely dependent on four remaining bird species (Kelly et al., 2006). These are endemic kereru (*Hemiphaga novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*) and native silvereyes (*Zosterops lateralis*), with silvereye and bellbird the two most important (Kelly et al., 2006). As a recent natural coloniser from Tasmania (Clegg et al., 2002), the silvereye are native, although any mutualism it has developed with native plants is novel. However, in many native forests often only one or two of these bird species are present (Robertson, 2007). These losses raise the potential for flow-on effects disrupting mutualisms such as seed dispersal and threatening the plant species that depend on these mutualistic interactions (Şekercioğlu et al., 2004, Kelly et al., 2010)

Comparisons of mainland – island patterns of fruit dispersal have been made with nikau (*Rhopalostylis sapida*), kotukutuku (*Fuchsia excorticata*), and karo (*Pittosporum crassifolium*). Results indicated that the dispersal of their seeds was reduced or slowed by a lack of frugivores on the mainland (Kelly et al., 2006). This suggests that the losses or absence of key bird species can reduce dispersal efficiency, especially for large-seeded fruiting species (Williams and Karl, 1996, Kelly et al., 2006). Further historic patterns of seed dispersal and forest regeneration can only be speculated at because of these absences (Clout and Hay, 1989, Atkinson and Cameron, 1993, Loiselle and Blake, 2002). This limits our current understanding about the processes that result in effective forest regeneration through bird-mediated dispersal.

1.3 Alien plants

Although often overlooked in comparison to invasive animals, the introduction of exotic plants into novel environments can often exceed that of animals in both number of species and their effects (Lodge, 1993, Vitousek et al., 1997, Keane and Crawley, 2002). New Zealand is no exception. A total of 24,744 plant species have been introduced since European colonisation (Duncan and Williams, 2002). Of these, 1,769 species have become fully naturalized in New Zealand and have formed populations that are self-maintained by seed or vegetative reproduction, or that occur repeatedly in wild or urban environments (Duncan and Williams, 2002). Naturalised species are often overlooked by ecologists with an interest in native habitats, as they typically form pioneer communities within disturbed habitats (Vitousek et al., 1996, Callaway and Aschehoug, 2000, Mack et al., 2000). It is not until they rapidly spread through native environments that they are perceived to become problem weeds (Vitousek et al., 1996, Callaway and Aschehoug, 2000, Mack et al., 2000). Widespread anthropogenic introductions of plants have thus received more intense scrutiny in recent decades following growing concerns that naturalized organisms impose detrimental effects on biodiversity (Levine et al., 2003, Simberloff, 2005, Rejmanek, 2000, Lodge, 1993, Kearns et al., 1998, Mills et al., 1993, Knops et al., 1999, Stinson et al., 2006).

1.3.1 Potential effects alien fruiting plants can have on frugivores

Alien plant species which become invasive weeds can negatively affect native biota through a variety of means, including disrupting mutualisms, altering resource availability and changing the quality of space available within ecosystems (Levine et al., 2003, MacDougall and Turkington, 2005). In particular, alien species can disrupt mutualistic plant–animal interactions, such as pollination and seed dispersal (Christian, 2001, Bjerknes et al., 2007, Kearns et al., 1998). In the worst – case scenarios, invasive weeds can reduce biodiversity by creating dense monocultures (Daehler, 1998).

A review by Bjerknes et al. (2007) found that there was high variability in the effects different invasive plant species have on pollination rates in native vegetation. They highlighted three possible outcomes: 1) invasive plant species attracted pollinators to the immediate area, thus increasing pollination of surrounding vegetation; 2) invasive plant species monopolised pollinator time and reduced pollination of the surrounding

vegetation; and 3) introduced plants did not affect pollinator behaviour. Despite the recognition of invasive species in affecting pollination regimes, few studies have determined if similar effects occur with fruiting vegetation and frugivores.

The lack of research on invasive fruiting plants is surprising, as many fleshy-fruited weeds can offer additional or alternative food sources for indigenous vertebrates (Williams and Karl, 1996). Native frugivores in a variety of locations have been observed regularly feeding on and dispersing seeds of introduced fruiting plants within their native ecosystems (White and Vivian-Smith, 2011, Voigt et al., 2011, Aslan and Rejmanek, 2010, Greenberg and Walter, 2010, Twigg et al., 2009, McCay et al., 2009, Gosper et al., 2006, Richardson et al., 2000, Simberloff and Von Holle, 1999, Drummond, 2005, Aslan, 2011). In some cases, native frugivores even showed a preference for introduced over native fruiting plants. Drummond et al. (2005) observed frugivore preference among four plant species, two introduced (*Lonicera tatarica* and *Rosa multiflora*), and two native plant species (*Cornus amomum* and *Viburnum opulus*) in Maine, USA. They found that frugivores preferentially consumed fruit from the invasive *L. tatarica* over the native *V. opulus*. Similarly, blackcaps (*Sylvia atricapilla)* in Europe have been observed shifting from native to introduced fruit species from early spring to summer, as native fruit becomes scarce (Debussche and Isenmann, 1990). Greenberg and Walter (2010) found that during winter 92% of seeds collected from the faecal samples of native birds were from non-native fruiting species in North Carolina, USA.

Apart from the direct effects on food supply, it has further been suggested that resources provided by invasive plants may affect the behaviour of some animals, such as changing their migration patterns, range, and survival (White and Stiles, 1992). For example, increased availability of fruit from invasive plants during winter has extended the winter range of the northern mockingbird (*Mimus polyglottos*) further north in the north-eastern USA (Stiles, 1982). Therefore the mutualisms between invasive plants and the animals that disperse them are likely important and help to facilitate the invasion of the weed species through the environment (Simberloff and Von Holle, 1999, Stiles, 1982).

1.3.2 Invasive fruiting plants in New Zealand

Most fruit dispersal systems are loose associations between seed-dispersers and fruiting plants. This normally results in very generalist foraging strategies by the

dispersers (Richardson et al., 2000). The generalist foraging behaviour of most frugivores is important for invasive dynamics where most relationships between frugivorous birds and invasive plants involve multiple dispersers (Richardson et al., 2000, Renne et al., 2002). New mutualistic seed-dispersal relationships can develop when native dispersers shift their foraging patterns to use the fruits of an invasive species, mimicking processes occurring in the plant's natural range (Gosper et al., 2005). Many bird species and in particular New Zealand's frugivorous avian fauna display generalist foraging strategies (Thorsen et al., 2011). Generalist dispersers have been observed dispersing invasive seeds at higher rates, it is therefore expected that generalist promote invasions through frugivory, therefore fleshy-fruited plants are often considered of higher environmental risk in ornamental, agricultural, or horticultural introductions than abiotically dispersed plants (Rejmánek and Richardson, 1996, Aronson et al., 2007).

Dispersal of adventive weeds into regenerating scrub by birds is considered one of the most common threats to indigenous forests (Timmins and Williams, 1987). With the increasing number of plants being introduced and eventually naturalizing within native forests it is important to understand how they will affect frugivores and in turn how this might affect the dispersal of both native and introduced plants (Gosper et al., 2005, Buckley et al., 2006).

1.4 Introduced birds

Not only have there been many extinctions of native frugivores in New Zealand but a number of exotic bird species have also been introduced in the past 150 years (Green, 1997, Heather and Robertson, 1998). Some of these introduced bird species are the native dispersers for the naturalised fruiting plants that have also been introduced into New Zealand (Snow and Snow, 2011). These disperser mutulisms have therefore not been entirely lost as the introduced plants have entered New Zealand. Naturalised frugivores also often consume the fruit of exotic plants, sometime at higher rates in comparison to native birds and, thus, can be a major vector in plant invasions (Williams and Karl, 1996, Mandon-Dalger et al., 2004). As invasive fruiting weeds can have detrimental effects on native forests, it is important to understand the dispersal processes occurring within habitats in relation to the dispersal dynamics of the introduced plant species.

There are at least 21 species of bird that have been naturalised in New Zealand through human intervention in the past 150 years that now have self sustaining populations in the wild (Green, 1997, Heather and Robertson, 1998). This includes 16 common passerine species (Heather and Robertson, 1998). However, naturalised bird species are commonly considered to provide relatively poor ecological services for native vegetation in comparison to native species (Kelly et al., 2006 Aslan, 2012). Of the introduced bird species only blackbirds (*Turdus merula*) are considered effective seed dispersers for vegetation in comparison to the other introduced birds (Clout and Hay, 1989, Williams and Karl, 1996, Kelly et al., 2006). Blackbirds have one of the largest ranges of any passerine bird species in New Zealand and have been observed foraging in dense native vegetation, highly urbanised environments and open pastoral farmland (Williams, 2006). Several other species have also been observed feeding on native fruit, such as dunnocks (*Prunella modularis*), Indian myna (*Acridotheres tristis*), song thrush (*Turdus philomelos*) and starling (*Sturnus vulgaris*), (Heather and Robertson, 1998, Clout and Hay, 1989, Williams and Karl, 1996). Finches (family: Fringillidae) have been observed feeding on fruit they are normally considered seed predators, chaffinchs (*Fringilla coelebs*) has been observed dispersing seeds in New Zealand (Williams and Karl, 1996). While a great deal is known about the foraging behaviour of these species within their native ranges, their precise role in any New Zealand ecosystem is poorly understood (Williams, 2006). However, a review from Kelly et al. (2006) on the ability of introduced species to act as dispersal vectors for native vegetation in New Zealand found that exotic bird species have generally not replaced declining endemics.

Although introduced birds are often considered inefficient dispersers for native vegetation they are sometimes the only dispersal vectors available. In the Hawaiian Islands almost all of the native seed dispersers are extinct or absent from native forests (Foster and Robinson, 2007). As in New Zealand, the Hawaiian Islands have gained many introduced bird species (Stone and Anderson, 1988). Since 1850, at least 58 species have been naturalized with self sustaining populations in Hawaii (Stone and Anderson, 1988, Pyle, 2002). This includes a number of frugivores; Japanese white-eye (*Zosterops japonicus*), red-billed leiothrix (*Leiothrix lutea*), Japanese bush-warblers (*Cettia diphone*), hwamei (*Garrulax canorus*), northern cardinals (*Cardinalis cardinalis*), spotted doves (*Streptopelia chinensis*), and Indian myna (Foster and Robinson, 2007). Many of the now naturalised birds act as the primary

dispersers of native seeds into exotic-dominated forests in Hawaii (Foster and Robinson, 2007). Indeed, most common understory plants in Hawaiian rainforests now depend on introduced birds for dispersal. It is likely that these introduced birds may actually facilitate maintenance and possibly restoration of native forests (Foster and Robinson, 2007). However, introduced frugivores in Hawaii were also observed frequently dispersing introduced fruiting species throughout native forests (Foster and Robinson, 2007). Thus, although they probably have positive effects on forest restoration in Hawaii there are also a number of negative aspects associated with their introduction.

To date, dispersal ecology has played a relatively minor role in invasion and restoration ecology research, and dispersal processes that result in the movement of invasive populations throughout landscapes is poorly understood (Westcott and Fletcher, 2011). Thus frugivore-mediated dispersal of invasive plants is an area of emerging importance in the weed management sector, highlighting a need for information on how frugivores, and in particular frugivorous birds, are assisting weed population dynamics and spread.

1.5 Thesis outline

The objectives of this thesis are to examine the mutualisms that occur between frugivorous bird species and the plant species they disperse. All experiments and observations were carried out in a native regenerating forest, Kowhai Bush, a 240 ha woodland near Kaikoura (173° 37' E, 42° 23' S). The forest interior consists of a varying aged flood-induced patchwork of successional stages differing in structure and species composition. The forest canopy is dominated by kanuka (*Kunzea ericoides*), with some manuka (*Leptospermum scoparium*). Along the eastern sections large areas of understory have been invaded and colonised by the noxious weed barberry (*Berberis glaucocarpa*). Extensive vegetation observations of Kowhai Bush are described in detail by Hunt and Gill (1979). All observations will be conducted during autumn 2011. This is the optimal time to observe frugivorous interactions as most plant species fruit during this time period. This was instrumental for all chapters.

Specifically, the three following questions are addressed in this thesis:

1. Does the removal of fruit (and thus a source of food) from an introduced plant species (barberry) affect the behaviour of an endemic frugivore (bellbird)?

2. Which bird species were the primary dispersers for barberry and how effective were they as dispersers?

3. Which bird species were important key dispersers for fruit-bearing plant species and what was the overall seed dispersal web in a native bush, Kowhai Bush?

In Chapter two, I experimentally test if *Berberis glaucocarpa* fruit was used as a food source by endemic bellbirds, and if the removal of fruit from this invasive species would affect the foraging and daily behaviour of bellbirds. The ecological literature is largely silent about the possibility of predicting how mutulistic interactions from an introduced fruit affect frugivore behaviour. Prior to the starting this thesis I observed bellbirds in Kowhai Bush feeding on barberry nectar, thus they do recognise barberry plants as a resource and may also use their fruit as a resource. Barberry is a highly invasive and noxious weed species (Froude, 2002, Rahman et al., 2003, Howell, 2008), that has large stands throughout Kowhai Bush. It is therefore important to understand how its removal will positively or negatively affect endemic birds.

In Chapter 3 I use a broader approach to determine which other bird species may be acting as key dispersal vectors for barberry. It has been proposed by Rejmánek (1996) that the presence of an efficient bird-disperser is a key predictor of the potential success a fleshy-fruited invasive species. Furthermore, the introduction of frugivorous species into New Zealand may have increased the likelihood that this introduced plant species will be successfully dispersed as one of them may feed on it. If this is occurring it could reduce the environmental resistance Kowhai Bush has against the spread of barberry.

In Chapter 4, I describe the frugivore seed dispersal dynamics in Kowhai Bush. Much focus in recent decades has been placed on forest regeneration and protection in New Zealand, however little is known about the introduced dispersal agents within

these forests and the how they are connected to dispersal systems within native forests (Kelly et al., 2006). Kowhai Bush is an interesting scenario as almost all large native frugivorous bird species are absent from this forest. Notable absentees from Kowhai Bush during autumn are kereru (*Hemiphaga novaeseelandiae)* and tui (*Prosthemadera novaeseelandiae*), which are both considered important seed disperser in other native forests in New Zealand. Medium sized introduced frugivorous bird species such as blackbirds and song thrushes are commonly observed throughout Kowhai Bush. Introduced birds have been observed dispersing fruit of introduced plant species at higher than expected rates throughout native forests in New Zealand (Williams and Karl, 1996). It is therefore expected that Kowhai Bush may have increased rates of dispersal of adventive weeds throughout its system. Observations were carried out to see which plant species' seeds frugivorous bird species were dispersing in Kowhai Bush.

Finally, in Chapter 5 I provide a general discussion and highlight the implications of my findings from the previous three research chapters and discuss the overall ramification of the results.

Chapter 2

Does the removal of an introduced fruiting plant modify frugivore behaviour?

2.1 Abstract

Chapter 2 was designed to test if the removal of an invasive alien plant's fruit affects a native seed disperser's behaviour. Observations were made to see if bellbirds (*Anthornis melanura*) changed their territory sizes, foraging and daily behaviours after an invasive plants fruit barberry (*Berberis glaucocarpa*) was removed from their territories. Observations were conducted during autumn, when barberry fruit was ripe. It was expected that if barberry is acting as a resource one or more of these behaviours would change. A total of 52 hours of direct observations of bellbirds were collected. During this time bellbirds were never observed feeding on barberry fruit. There were no significant changes to any of the bellbirds behaviours after the removal of barberry fruit. A total of 3454 foraging observations were collected, bellbirds fed on 11 different food sources. This included invertebrates, fruit, nectar, and honeydew. Invertebrates formed the majority of observations (82.7%), followed by fruit (15.7%). Honeydew 0.5% and nectar 1.1% only made up very small proportions of the diet. A total of 6142 bellbird behavioural observations were collected. Bellbirds spent the majority of their time feeding (56%), followed by resting (14.5%), locomotion (11%), calling (10%), preening (8%) and socialising (0.5%). On average bellbird territory sizes were 2678 ± 31 m^2 (range 1347 to 5142 m^2). If barberry was removed from areas that bellbirds inhabit it is unlikely to negatively affect their behaviour during autumn. However its subsequent spread through native forests could reduce habitat quality for native birds.

2.2 Introduction

One exotic fruiting species that is currently expanding its range throughout New Zealand, in particular in the North Island and north–eastern areas of the South Island, is *Berberis glaucocarpa* or barberry (Sykes, 1982). Introduced in 1916, barberry has since become a widespread noxious plant species (Froude, 2002, Howell, 2008). Birds act as the main dispersal vectors for barberry, although introduced possums (*Trichosurus vulpecula*) can potentially disperse seeds (Timmins and Williams, 1987, Williams and Karl, 1996, Williams et al., 2000). During the flowering season of barberry from September to November 2011, endemic bellbirds and native silvereyes were regular observed visiting flowers (*pers. obs.*). Since both of these bird species recognise barberry flowers as a resource, it is plausible that they also use its fruit as a resource. Observations in the literature, in particular Bjerknes et al. (2007) review, suggest that if barberry fruit is acting as a resource for endemic frugivores, it has the potential to increase the frugivore's fitness and influence their foraging behaviour. This in turn could cause negative secondary effects for native vegetation by altering important endemic disperser-plant mutualisms. The opposite may occur and its removal, from native systems could have negative effects on endemic biota by reducing available food.

If disruption of frugivore mutualisms by barberry are occurring this could have important effects within native ecosystems, in particular within early successional communities where pollination and seed-dispersal mutualisms are important for maintaining structure and diversity (Bond, 1994, Kearns et al., 1998). By understanding how introduced plants affect both native frugivores and fruiting plants we can further potentially predict what effect they will have within native forest. It is therefore important that we understand how invasive plants could affect frugivores and fruiting plants connections.

Many studies have observed or tested how the loss or introduction of a dispersal vector affects fruiting vegetation dispersal (Wotton and Kelly, 2011, Şekercioğlu et al., 2004, Wang et al., 2007), yet few studies have observed the reverse where an introduced fruiting plant affects frugivore behaviour (Gosper et al., 2005). No studies have tried to directly test whether or not an introduced fruiting plant directly influences endemic frugivores behaviour by acting as a resource and how subsequent removal of the fruit could positively or negative affect frugivore fitness.

The purpose of this study was firstly to investigate how important fruit from an invasive plant species, barberry, was as a resource for an endemic frugivore, bellbirds (*Anthornis melanura*). Secondly, does barberry fruit removal affect the foraging or other behaviours of bellbirds?

To investigate these questions, bellbird diet, time budget and territory sizes were sampled over a four month period during barberry's fruiting season, autumn 2011, in a regenerating native bush, Kowhai Bush near Kaikoura.

Specifically, three questions were examined:

1. What were bellbirds feeding on in Kowhai Bush and did bird foraging behaviour alter after the removal of barberry fruit?

2. Did birds change their daily activities after barberry fruit was removed?

3. Did birds change their territory sizes after barberry fruit was removed?

2.3 Methods

2.3.1 Study site

All observations were carried out at Kowhai Bush (173° 37' E, 42° 23' S), a 240 ha regenerating native woodland near Kaikoura (Fig. 2.1). The areas to the north and east of Kowhai are cleared for agricultural use while the areas to the south and south-west are river shingle plains (Fig 2.1). However, Kowhai Bush is connected to lowland podocarp – hardwood forests by a narrow strip of vegetation running along its north-western edge (Fig 2.1). This has created a link between the two systems and probably promotes dispersal of many different native bird species between them. The sharp boundaries around Kowhai Bush have created an ecological island within the farmland.

Kowhai Bush's forest interior consists of a flood-induced patchwork of successional stages of differing age, structure and species composition. The forest canopy is 5-12 m high dominated by kanuka (*Kunzea ericoides*), and in areas manuka (*Leptospermum scoparium*). A narrow strip of kanuka/broad-leaf forest covering river gravels is on the north-eastern side. Along its eastern margins large areas have been invaded by introduced hedge row species barberry and hawthorn (*Crataegus*

monogyna) from surrounding farm land. Extensive vegetation observations of Kowhai Bush are given in Hunt and Gill (1979).

Figure 2.1, the area highlighted with a white border is Kowhai Bush, Kaikoura. All observations were collected for Chapters 2, 3 and 4 in this area. Base map sourced from Google maps.

2.3.2 Study species

Bellbirds are a common endemic passerine species found throughout New Zealand. They are both an important pollinator, and disperser of native fruiting vegetation (Ladley and Kelly, 1996, Clout and Hay, 1989, Kelly et al., 2010, Kelly et al., 2006). Bellbirds feed on and disperse many fleshy-fruited plants in New Zealand, forming mutualisms with these species (Lord et al., 2002). Bellbirds are one of the few endemic species that has relatively widespread populations with year round high numbers in native forests (Heather and Robertson, 1998), and are considered one of the four most important fruit dispersers in New Zealand (Kelly et al., 2010). However they have been observed feeding on introduced fruit from plants *Cornus capitata* (Medway, 2009), *Arbutus unedo*, *Ilex aquifolium* and *Leycesteria formosa*, (Williams and Karl, 1996). In Kowhai Bush, bellbirds are the only endemic species of frugivore that occur year round in high numbers. Although low numbers of tui (*Prosthemadera novaeseelandiae*) were observed in Kowhai Bush during spring and early summer

they had departed by autumn. Kereru (*Hemiphaga novaeseelandiae*), which are important endemic seed dispersers particularly for large seeds in New Zealand (Kelly et al., 2006), were absent from Kowhai Bush during this study and in previous observations.

Identification between bellbird sexes is relatively easy as there are significant morphological differences between male and females. Females have white cheek stripes, are paler gray-green, and approximately 25 g (Heather and Robertson, 1998). Males are much larger (approximately 32 g) and have dark green plumage with a purple hue across the head. During the nestling periods female birds need to spend more time feeding on invertebrates than males to keep up with the high energetic demands chicks impose, for bellbirds nesting occurs from approximately September to February and both males and females help raise the chicks (Heather and Robertson, 1998). Since the study reported here was carried out from mid February till the end of May it is unlikely that any males or females were still tending chicks. None of the birds used in this experiment were observed with chicks and foraging behaviour between males and females was unlikely to differ.

The invasive plant species used for the experiments was barberry (*Berberis glaucocarpa*). Endemic to Eastern Europe and the Himalayas, it was introduced to New Zealand in 1916 as a hedgerow plant (Roy et al., 2004). It soon become naturalised and spread throughout much of New Zealand (Owen, 1997, Rahman et al., 2003). It has since been classified as an invasive and noxious weed species (Froude, 2002, Rahman et al., 2003, Howell, 2008). Barberry can be found throughout Kowhai Bush's Eastern sections (Fig. 2.2). Hedge rows of barberry are also found along Kowhai Bush's eastern sections within farm land and were likely the parental populations that have subsequently been dispersed into Kowhai Bush (Fig. 2.2). Barberry's invasive success is attributed to both its life history traits and its ability to tolerate a wide range of conditions. Barberry's large size (up to 7 m), coupled with its ability to produce large quantities of long-lasting seeds, help sustain populations in competitive environments (Roy et al., 2004). Fruit is dispersed by vertebrates, predominantly birds. It has been suggested that barberry may be able to regenerate beneath the closed canopy of some short forest types and compete with native vegetation (Williams and Timmins, 1990, Sullivan et al., 2007). If left unchecked in

open or regenerating habitats it can rapidly colonise these areas and replace other shrub land species (Sullivan et al., 2007).

Flowering of barberry in Kowhai Bush occurred from October to November. Flowers are small, yellow and attach in bundles of 4-12. Pollination is predominantly performed by invertebrates although bellbirds and silvereyes (*Zosterops lateralis*) were observed visiting flowers in Kowhai Bush. Fruiting season at Kowhai Bush lasts from the end of February until June. Fruit are small, 8 mm in diameter, round, black/purplish, with a white bloom.

Figure 2.2, the area within the white line is Kowhai Bush. Areas shaded in white and black along the eastern sections of Kowhai Bush have been invaded by barberry and subsequently where all the bellbird behaviour observations were made for Chapter 2. Base map sourced from Google maps. Areas with white dashed lines are mixed species hedge rows that include barberry and were likely the original parental populations for barberries spread.

2.3.3 Experimental set up

From 1 January 2011 till 15 May 2011, bellbirds in Kowhai Bush were mist netted and colour banded. Mist netted birds' gape was also measured. Only colour banded individuals that had set up territories within areas of barberry were used for the experiment. Bellbirds are generally highly territorial year round and the observed birds in the study remained in their territories (Craig and Douglas, 1986). However, outside the breeding season territories are sometimes relaxed and birds occasionally form small foraging flocks of either adult females and juveniles or adult males (Heather and Robertson, 1998). Prior to using a bird in the experiment they were observed over a period of 7-14 days to see if they remained in the same area and had a claimed territory. Many observed banded birds were vagrants and only remained in one area for a short period (3-4 days) before moving to a new area. It was easy to distinguish which birds were territory holders as they would avidly defend territories by confronting intruding birds with both calls and physical interactions, flying at or chasing the intruder, similarly they were normally found within the same area of bush each time. This reduced the likelihood that an experimental bird would turn out to be a vagrant bird and disappear during in the experimental observations. A total of 18 birds (8 males and 10 females) were used for the experiment. Birds were split into two groups, control and test birds. This was evenly split between 9 control and 9 test birds, 4 males and 5 females per site. Test birds had all the barberry fruit removed from their territories while control birds had no barberry fruit removed. However some foliage was removed from barberry plants in control bird territories to control for habitat modification. Bellbird observations were carried out over a 106 day period from 15 February to 1 June. During this time only four observational periods could be undertaken. An observational period was defined as the total time a group of experimental birds was followed. During each observational period groups of only four or six birds were observed, this was evenly split between control and test birds. If more birds were followed the task of collecting data and observing the daily behaviour of each bird became too difficult. To see if bellbirds were influenced by the removal of barberry, I first followed each individual bird for a minimum of 7 days, although some individuals were observed up to 10 days if conditions were favourable. When a bird was spotted, key behaviours were verbally noted onto a hand held recorder. Each time a bird was observed its position was also recorded on a gridded (15x15 m) map. This allowed me to determine the boundaries of the bird's territory

and subsequently which barberry fruit was to be removed within its territory. Several observations (mean = 3, range 1 to 8) were made on each bird each day. Each observation was the total time that a bird could be followed for before visual contact was lost with it. The audio files were played back using the program VLC media player. Instantaneous sampling with 30 second intervals was used to estimate the percent daily activity and foraging behaviour from the audio recordings. This method and time interval were chosen as it separated foraging observations into discrete events but still allowed me to gather enough data given the low number of daily encounters (see Altmann (1974) and Martin and Bateson (1993) for instantaneous sampling methods). The observations for a particular bird on a designated day were then summed together to give the total time, minutes, that the bird was observed for on that day. A minimum total of 5 minutes of observations was collected for each bird on each of the 7 days. If the observed bird was recorded for less than 5 minutes each day, it is unlikely that enough data could be collected to observe significant changes in behaviour. Birds were also observed for a maximum of 15 minutes per observation before contact was terminated. This was to avoid biased sampling since several behaviours were easer to observe over longer periods of time than others.

On the 8th day the total ripe fruit, unripe fruit and damaged fruit on barberry plants within the territory of all the test birds was recorded then removed. Due to the size and position of many of the plants it was not possible to directly record all ripe, unripe and damaged fruit. Instead to estimate these variables 25 bundles of fruit were selected at random on each plant, if there were fewer than 25 bundles on the plant they were all recorded. The total number of fruit on each bundle was recorded. This was then totalled before being divided by the number of bundles recorded to give an average number of fruit per bundle. From each bundle of fruit the total ripe and damaged fruit was also recorded. To work out the average number of ripe and damaged fruit per bundle. The total numbers of bundles on each plant was then counted. I then multiplied the total number of bundles on the plant by the average number of ripe and damaged fruit per bundle. To give an estimated total number of ripe and damaged fruit on each observed plant. An ANOVA was run on 20 randomly chosen plants at the start of the fruiting season to see if plants had significantly different fruit per bundle, ripe fruit and damaged fruit. If plants were not significantly different it would have been possible to select 20 plants at random and used them as template to estimate the total fruit per bundle, ripe fruit and damaged fruit per birds'

territory during each observational period. However there were significant differences between the available ripe fruit (F= 37.99, df= 19, P=0.001), damaged fruit (F= 8.73, df=19, P=0.003) and available fruit per bundle (F= 17.44, df=19, P=0.001) on each plant. Therefore the above data had to be collected from each individual plant in order to gain accurate estimations for fruit availability per bird's territory. After each test birds had been observed for a minimum of one week the total number of ripe fruit, damaged fruit and fruit available fruit per bundle was recorded on each individual plant within the observed bird's territory before the fruit was removed. This fruit was removed using a hook attached to the end of a 2 m long pole to pull each bundle of fruit off the barberry plant. The fruit was then collected off the ground and removed from the territory. It was not possible to collect all the fruit off the ground however it was unlikely that bellbirds would feed on any fruit that was left on the ground as bellbirds are an arboreal species which were never once observed feeding on the ground in Kowhai Bush. In control territories, the same recordings were made for the fruit but only some non-fruiting foliage was removed from barberry plants. Observed birds were then given a day to acclimatise to their new environment. Using the same procedures as mentioned previously birds were again observed over another minimum 7 day period.

Data collected from the time budget observations were also used to compare changes in each bellbird's foraging behaviour. When a bird was recorded feeding during a 30 second time interval the observed food was also recorded until visual contact with the bird was lost.

2.3.4 Behavioural observations

Data on bellbird foraging behaviour was collected using direct observations gathered during the time budget observations. Every feeding event was allocated to one of the following food categories: (1) nectar (plant species noted), (2) fruit (plant species noted), (3) definite invertebrate (where the invertebrate could be seen), (4) probable invertebrate (where the food item could not be seen but where the beak movement and foraging behaviour was consistent with invertebrate foraging), and (5) honeydew.

At the start of each 30 second observational sampling period, when the bellbird was visible, its activity was placed in one the following activity categories following Murphy and Kelly (2001) methods: (1) feeding, which included swallowing fruit, gleaning through flowers and honeydew or rapidly gleaning through a tree in search

of invertebrates; (2) moving/ locomotion, flying, walking or hopping; (3) preening; (4) resting; (5) calling; and (6) socialising, including aggression, copulation and other social contact.

For territory size, the position of the observed bird within Kowhai Bush was recorded during every observation onto a 15x15 m gridded map of Kowhai Bush to establish the area of their territory.

2.3.5 Analysis

The software package R 2.13.2 (2011-09-30) was used for all statistical analysis. All graphs were created using the program SPSS.v16-EQUiNOX. To test for changes in behavioural and foraging observations, comparisons were made between sites, control and test. Within each site, tests were made across time, pre- and post-barberry removal periods. The key aim for all the observations was to see if these was a significant site x time interaction. If there is a significant site by time interaction for the observations it will indicate that barberry fruit removal changed bellbird behaviour. Generalized Linear Models (GLMs) were run on all data sets to determine which explanatory variables had a significant effect.

Low feeding observations on several fruiting plant species made it unfeasible to run individual statistical tests on each of them. Therefore, the fruiting species which had low numbers of observations were grouped together as "other fruit". *Coprosma robusta* was the only fruit species that was frequented enough to test on its own in GLMs. Analyses could not be run on honeydew and nectar because of the low numbers of observations collected on these two food sources.

To analyse the foraging and daily behaviours data, a binomial GLM model was used. This tested the proportion of all observed behaviours which fitted into category being tested (eg proportion feeding, etc.). To achieve this in r the function `cbind` (function bellow) was used to bind together the two numerical vectors as columns to make a matrix, for example.

```
Glm1<-glm(cbind(feeding,(totalobservations -
feeding))~time*site, family= quasibinomial)
```

Due to overdispersion, quasi-binomial GLMs with the more conservative "F" test were used on the data sets. The quasi-binomial GLMs were used to test which explanatory variables had a significant effect for four diet items; probable

invertebrates, confirmed invertebrates, *C. robusta* fruit and other fruiting vegetation. In addition, a quasi-binomial GLM was used to test which explanatory variables had a significant effect on daily activities; feeding, moving/ locomotion, preening, resting, calling and socialising.

The appropriate territories for each bird were calculated using a standard estimator MCP (Minimum Convex Polygons) by connecting the outer points of the mapped locations of the birds (Bas et al., 2005, White and Garrott, 1990). To check for normality qqnorm plots were used in R. The data were normally distributed so a gaussian GLM was used to see if territory size changed after fruit removal.

2.4 Results

A total of 52 hours of direct visual observations were collected from the observed birds, each individual observation on average only lasted for 3 minutes 27 seconds before visual contact was lost with the bird. At the end of each 7 day observational period each bird was on average observed for a total of 1 hour 28 minutes. Of the 52 hours of observations birds were observed feeding for 29 hours, during this time bellbirds were never observed feeding on barberry fruit.

Overall, bellbird territories were on average 2678 ± 31 m² (range 1347 to 5142 m²) and contained a mean of 5447 ± 948 ripe barberry fruit (range 239 to 9456 fruit). On average each bird's territory contained 15 ± 1.5 barberry plants (range 4 to 26 plants). There was a higher percentage of ripe fruit at the end of the fruiting season than at the start (Fig. 2.3). The percentage of damaged fruit on barberry plants remained low from the start of observations until the end of observations (Fig. 2.3).

2.4.1 Foraging observations

A total of 3454 foraging observations were collected. Bellbirds were observed feeding on a total of 11 different food sources, including invertebrates, fruit, nectar and honeydew (Table 2.1).

As bellbirds never feed on barberry fruit it would be surprising to find any effects. There were no significant site x time interactions for the tested foraging observations; probable invertebrates, confirmed invertebrates, *Coprosma robusta* and other fruit (Table 2.2). There was no significant difference between the sites for probable invertebrates, confirmed invertebrates and *Coprosma robusta* (Table 2.2). However there was a significant difference between test and control bird visitation rates to other

fruiting species (Table 2.2). This was most likely because control birds feed on a larger range of fruiting species at higher rates than test birds. Control birds were observed feeding on *C. rhamnoides* and *C. propinqua* whereas test birds did not feed on these fruit species (Table 2.1). This may represent differences in the availability of these rarer fruit in the territories of test vs control birds. There were no significant differences across time for all the observed tests; probable invertebrates, confirmed invertebrates, *Coprosma robusta* and other fruit (Table 2.2).

No significant differences between control and test bird diets were observed due to barberry fruit removal. Therefore, the foraging observations were combined for both control and test birds to show overall bellbird diet during autumn. Invertebrates formed the largest proportion of the diet (82.7% in total). This was split between probable invertebrates, and confirmed invertebrates (Table 2.1). Fruit made up a smaller total combined proportion of foraging events (15.7% in total) in comparison to invertebrates (Table 2.1). *Coprosma robusta* formed the vast bulk (13.52% in total) of fruit foraging observations (Table 2.1). The remaining fruiting plants bellbirds fed on were *C. propinqua x robusta, Coprosma rhamnoides, Coprosma propinqua, Coprosma grandifolia, Melicytus ramiflorus* and *Ileostylus micranthus* (Table 2.1).

Overall honeydew formed a very small proportion of foraging observations (0.5%) (Table 2.1). Due to the forest composition in the study site, there is little available habitat for scale insects and little honeydew is available. Similarly nectar formed a small proportion of foraging observations (1.1%) (Table 2.1). Due to the time of year there were few flowering species in Kowhai Bush.

2.4.2 Bellbird time budgets

A total of 6142 bellbird behavioural observations were made. Similar to foraging observations, there was no significant interaction between time and site for bellbird daily activities (feeding, moving/ locomotion, preening, resting, calling and socialising) (Table 2.3, Fig. 2.5). Similarly there were no significant differences between the sites or across time for the birds' daily activities (Table 2.3, Fig. 2.5).

Because there was no significant difference between control and test birds, daily time budget observations were combined. Collectively, birds spent 56% of their time foraging (Fig. 2.5). Resting was the second most common daily activity (14.5%) (Fig. 2.5). Observed birds quickly moved to confront intruders, during socialising events or moving between patches of resources, birds spent 11% of their time in locomotion

(Fig. 2.6). Calling was a slightly less common activity (10% of observations), followed by preening (8%) (Fig. 2.5). Socialising made up only a small fraction of daily activities (0.5%) (Fig. 2.5).

2.4.3 Territory sizes

There was no significant interaction between site by time for the birds' territory sizes (Table 2.4). On average bellbirds territory sizes were 2678 ± 31 m² (range 1347 to 5142 m²). However there was a significant difference between sites (Table 2.4). This was likely because control birds had larger territories than test birds. Test birds had on average a territory size of 2443 ± 230 m² (range 1347 to 4180 m²). In comparison control bird had a larger average territories size of 2980 ± 241 m² (range 1375 to 5142 m²).

2.4.4 Bellbird gape sizes and mean diameter of barberry fruit

Barberry fruit in Kowhai Bush had a mean diameter of 7.6 ± 0.13 mm, n = 25 (range 6.1 - 8.2 mm; Fig 2.4). Bellbirds caught had a gape of 7.9 ± 0.78 mm, n=15 (range 5.6 - 8.8 mm, Fig. 2.4). Therefore, bellbirds with a mean gape size of 7.9 mm could eat at least 57 % of the fruit on barberry plants. The largest bellbird gape could eat all of the measured barberry fruit (Fig. 2.4).

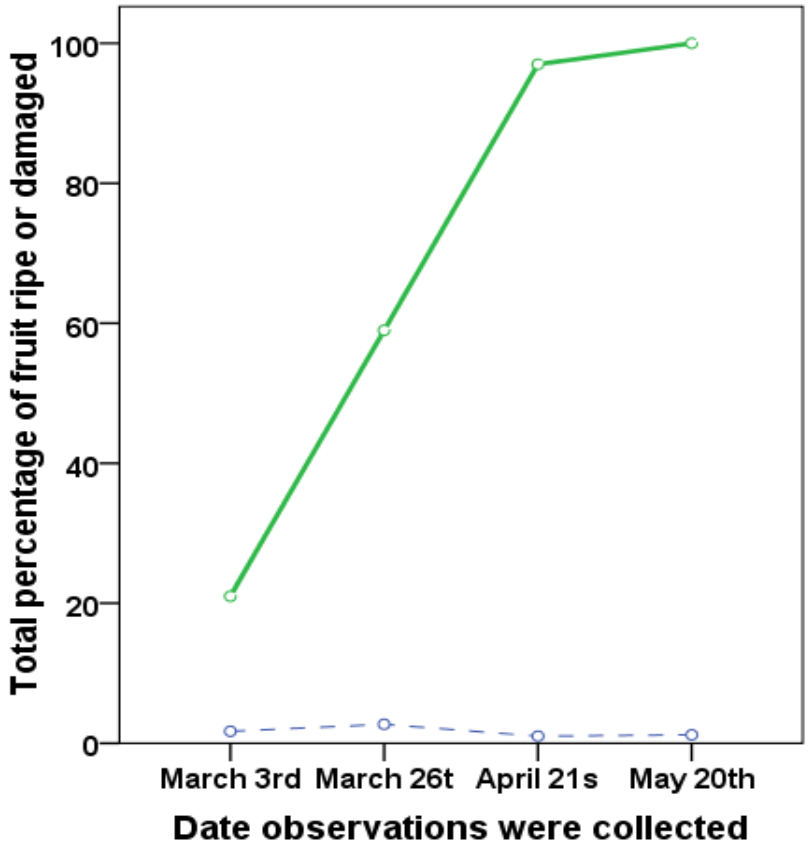

Figure 2.3 Barberry fruit on plants which were ripe or damaged through the 2011 season at Kowhai Bush. Solid line is percentage of fruit that is ripe, dashed line is percentage of fruit that was damaged.

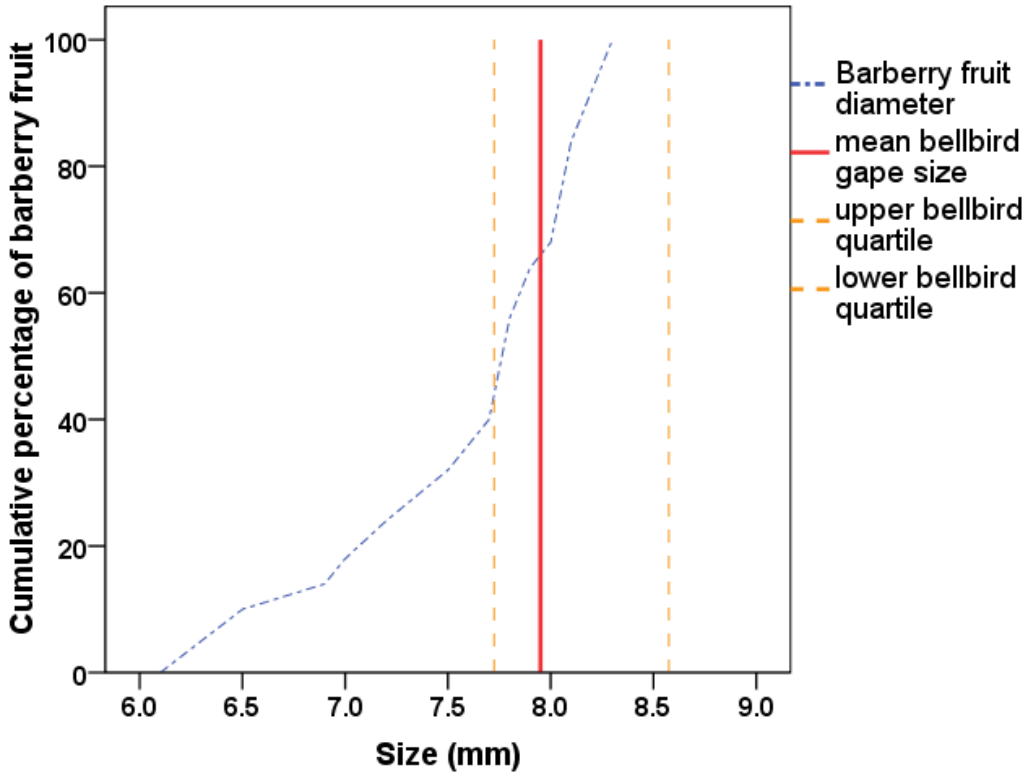

Figure 2.4 Cumulative percentage of barberry fruit collected at Kowhai Bush and mean bellbird gape size. X axis is given in mm diameter for both fruit and bellbird gape size. The 25th and 75th percentiles for bellbird mean gape size are presented as the straight dashed lines and mean size for bellbird gape size is the solid line. Barberry mean fruit size is presented as the curved irregular dashed line.

Table 2.1. Bellbird diet (% of dietary items) at Kowhai Bush in March to May 2011. Sites are split between test birds (fruit removed) and control birds sites. Each site is split into, pre and post removal, pre removal represents all observations before barberry fruit was removed from test bird territories. No fruit was removed from the control territories. The mean across all observations is presented. The numbers of observations during each period is given at the top.

Percentage of foraging observations for control and test birds						
		Test birds		**Control birds**		
		Pre barberry removal N=1082	Post barberry removal N=914	Pre barberry removal N=781	Post barberry removal N=677	Mean across all observations N=3454
Invertebrates	Confirmed invertebrates	9.5	5.9	6.9	9.2	7.9
	Probable invertebrates	75.0	77.8	74.9	70.0	74.8
Fruit	*Coprosma grandifolia*	0.2	0.1	0.1	0.7	0.3
	C. propinqua	0	0	0.4	0.3	0.1
	C. propinqua x robusta	1.0	0.7	2.7	0.7	1.2
	C. rhamnoides	0	0	1.0	0	0.2
	C. robusta	13.8	13.6	11.1	15.8	13.5
	Ileostylus micranthus	0	0.5	0.6	0	0.3
	Melicytus ramiflorus	0.4	0.0	0	0	0.1
Flowers	*Hebe* sp	0	0	0	0.6	0.1
	Pseudopanax arboreus	0	0.3	1.8	2.4	1.0
Honeydew	Honeydew	0.2	1.1	0.4	0.3	0.5

Table 2.2, Quasi-binomial Generalised Linear Models for the proportion of feeding observations devoted to various food types; confirmed invertebrates, *Coprosma robusta*, other fruit and probable invertebrates. The models time (before and after removal) and site (removed or not removed) are presented in combination with the time by site interaction.

Observed behaviour	**Model**	**d.f.**	**Deviance**	**F**	***P***	**% Explained**
Confirmed invertebrates	Time	1	1.53	0.39	0.54	1.01
	Site	1	0.01	0.00	0.96	0.01
	Time:Site	1	10.06	2.57	0.12	6.65
	Residuals	31	139.78			
Coprosma robusta	Time	1	2.51	0.22	0.64	0.67
	Site	1	0.11	0.01	0.92	0.03
	Time:Site	1	4.33	0.38	0.54	1.16
	Residuals	31	366.89			
Other fruit	Time	1	0.16	0.03	0.87	0.08
	Site	1	34.30	5.81	**0.02**	16.28
	Time:Site	1	4.61	0.78	0.38	2.19
	Residuals	31	171.60			
Probable invertebrates	Time	1	0.09	0.01	0.92	0.03
	Site	1	5.81	0.59	0.45	1.77
	Time:Site	1	6.48	0.65	0.42	1.97
	Residuals	31	316.42			

Table 2.3, Quasi-binomial Generalised Linear Models for proportion of all behavioural observations spent in particular activity types: calling, feeding, locomotion, preening, resting and socialising. The models time (before and after removal) and site (removed or not removed) are presented in combination with the time by site interaction.

Observed behaviour	Model	d.f.	Deviance	F	*P*	% Explained
Calling	Time	1	6.37	0.43	0.52	1.41
	Site	1	7.45	0.50	0.48	1.65
	Time:Site	1	20.54	1.38	0.25	4.55
	Residuals	31	451.77			
Feeding	Time	1	6.07	0.38	0.54	0.10
	Site	1	7.09	0.44	0.51	0.09
	Time:Site	1	18.58	1.16	0.29	0.05
	Residuals	31	508.09			
Locomotion	Time	1	0.45	0.43	0.52	0.58
	Site	1	0.52	0.50	0.48	0.68
	Time:Site	1	0.02	1.38	0.25	0.03
	Residuals	31	75.76			
Preening	Time	1	0.29	0.05	0.83	0.37
	Site	1	0.34	0.06	0.82	0.36
	Time:Site	1	12.10	1.94	0.17	0.08
	Residuals	31	213.11			
Resting	Time	1	0.05	0.01	0.93	0.03
	Site	1	0.06	0.01	0.92	0.03
	Time:Site	1	0.04	0.01	0.93	0.02
	Residuals	31	185.05			
Socialising	Time	1	0.25	0.12	0.73	0.37
	Site	1	0.29	0.14	0.71	0.44
	Time:Site	1	8.38	4.06	0.06	12.59
	Residuals	31	57.65			

Table 2.4, gaussian Generalised Linear Models bellbird for the changes in territory sizes. The models time (before and after removal) and site (removed or not removed) are presented in combination with the time by site interaction.

Model	d.f.	Deviance	Pr(>|Chi|)	% Explained
Site	1	4514062	**0.04**	11.7
Time	1	33800	0.86	0.1
Site:Time	1	16560	0.90	0.0
Residual	30	34015068		

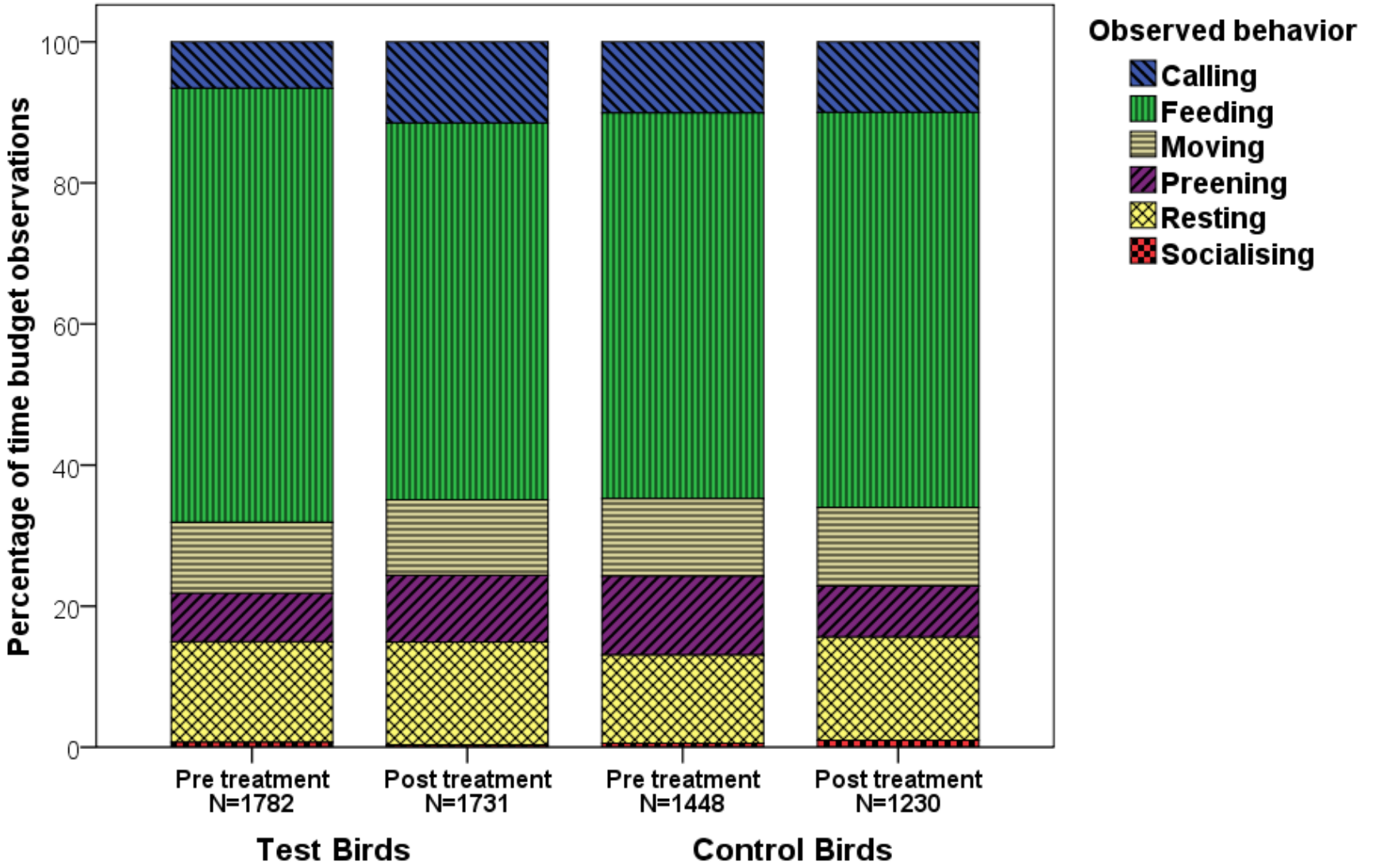

Figure 2.5, Observed bellbird time budget (% of time spent) at Kowhai Bush in March to May 2011. Birds are split between test and control. Pre-barberry removal represents all observations before barberry fruit was removed from test bellbird territories. Post barberry removal is all observations after the removal of barberry from territories. No fruit was removed from the control territories. The numbers of observations during each treatment are given at the bottom of the figure.

2.5 Discussion

Bellbirds were never observed feeding on barberry fruit even though the fruit appears nutritious, is eaten by other birds and within the size range bellbirds can swallow. These observations are reflected in the results, bellbirds did not significantly alter their foraging, other behaviours or territory size in any way after fruit removal. Therefore if barberry was to be removed from Kowhai Bush we would expect no effect on bellbirds foraging and other behaviours during autumn.

2.5.1 Bellbird foraging behaviour in Kowhai Bush

The storage and use of energy in birds exceeds that of all other vertebrates (Blem, 1976). Therefore, a bird's daily foraging and energy intake is exceptionally important for survival. In particular, autumn is a vital time of the year for energy intake, because many birds need to increase fat storage and energy intake prior to migration or for the coming winter when many resources may become scarce (Benson et al., 2005, Bairlein, 2002). Further, both adults and juveniles in some species need to increase proteins and carotenoids intake to replace energy lost during moult and to promote increased growth (Ricklefs, 1968).

Bellbirds at Kowhai Bush spent a large percentage of their day foraging, with invertebrates, fruit, nectar and honeydew making up their diet. Invertebrates formed the bulk of foraging observations (83%). High insect feeding year round and during autumn are not unexpected as invertebrate species are rich in crude protein, crude fat, carotenoids, minerals, amino acids, and vitamins (Bernard et al., 1997, Finke, 2002, Eeva et al., 2010). This can help birds during moult. During the study several of the observed birds underwent this process. Moult involves first shedding then replacing plumage, which uses large quantities of energy, minerals and carotenoids (Murphy and King, 1992, Surai et al., 2001, Goodwin, 1986, Brush, 1990, Eeva et al., 2010).

Seasonal breeding may have influenced foraging behaviour. A study by Bailey (1985) demonstrated that non-breeding male *Aythya americana* had higher protein reserves going into winter than breeding males which expended energy defending territories post breeding season. Non-breeding *Aythya americana* males were able to meet seasonal protein requirements more easily. Possible correlations could be drawn between bellbirds and *A. americana* males. Both male and female bellbirds actively co-defend a territory during their breeding season. If male and female bellbirds

expend large quantities of energy during the breeding season defending there territory it is plausible they need increased protein intakes to recover energy that was expended during territory defence.

Previous studies have also observed bellbirds primarily foraging on invertebrates during autumn (O'Donnell and Dilks, 1994, Williams and Karl, 1996, Murphy and Kelly, 2001). In Murphy and Kelly (2001) observations invertebrates made up 78% of bellbirds diet in April. Similarly O'Donnell and Dilks (1994) observed invertebrates making up 74.8% of bellbird total yearly daily diet. These similar results give confidence that the Kowhai Bush sampling gives a good indication of bellbird diet.

Fruit was observed to only form 16% of the observed bellbird diets. Although fruit did not form a large proportion of their diet, birds still regularly feed on fruit. Fruit is an important resource for sugars, lipids and protein which is important for birds entering winter (Bairlein, 2002, Stiles, 1993). Fruit is less important to birds during the breeding season and post breeding season as it typically contain lower levels of protein which are needed for reproduction, moult and or growth (Levey and Rio, 2001). Preference ratios are a good indicator for favourability of a particular resource by foragers (Forsyth et al., 2005, Loehle and Rittenhouse, 1982, Forsyth et al., 2002). However, too little information was collected of fruiting vegetations abundances to accurately calculate what bellbird preferences were. However general observations could be made and the relative preferences for some of the fruiting species could be suggested. *Coprosma robusta* represented the bulk of the fruit foraging observations and bellbirds showed a high preference for this fruiting species over most others. *C. robusta* was observed in high abundance in all of the bellbird territories and was one of the most common fruiting species in Kowhai Bush. The remaining fruiting species, *C. propinqua x robusta, C. propinqua, C. rhamnoides, C. grandifolia, Melicytus ramiflorus* and *Ileostylus micranthus* each only made up a small fraction of bellbirds diets. In many cases observed birds did not have one or more of these fruiting species within their territories however they did show marked differences in their preferences for these fruiting species. *C. propinqua* and *C. rhamnoides* had similar medium to low abundances in bellbird territories. Overall birds showed relatively low preferences for these two species although they were available to most of the observed birds. *C. grandifolia* had lower abundances than these previous *Coprosma* species, birds did visit plants and showed higher preferences for its fruit. Similarly *C. propinqua x robusta* had relatively low abundances in birds territories but birds had a relatively

high preference for *C. propinqua x robusta* fruit. In areas *Melicytus ramiflorus* was present in medium abundances and offered high concentrations of fruit on the available plants for foraging birds. However bellbirds showed low preferences for *M. ramiflorus* fruit. *Ileostylus micranthus* was very un-common and fruiting plants were only found in three of the bird territories. Yet these birds showed very high preferences for its fruit and were observed regularly feeding on its fruit.

Honeydew was observed in bellbird diets at very low levels (0.5%). The number of trees containing scale insect colonies was very low and similar to several of the fruiting plants, was only found in a limited number of bird territories. Very few observations were made of birds feeding on honeydew. Wasps *Vespula* spp were also commonly observed feeding on the available honeydew. This could reduce the amount of available honeydew and reduced the overall energetic value gained from feeding on it by increasing overall search time. Several other papers have also observed bellbirds foraging on honeydew at relatively low levels during autumn. Murphy and Kelly (2001) observed a significant difference between bellbird monthly foraging on honeydew. During April honeydew only made up 2% of bellbird diets. Similarly O'Donnell and Dilks (1994) observed bellbirds foraging on honeydew at relatively low levels throughout the year.

Nectar also did not play a large role in bellbird diet in autumn. During spring nectar has been observed making up a substantial part of bellbird diets (O'Donnell and Dilks, 1994, Murphy and Kelly, 2001). However during autumn there were very few plant species flowering in Kowhai Bush. It was not until late May, when the last sets of birds were being observed, that *Pseudopanax arboreus* flowered on a limited number of trees. However in areas that it was available bellbirds showed very high preferences for *Pseudopanax arboreus* nectar and observed birds could often be found feeding on their flowers. Similarly *Hebe* spp were only recorded flowering on a limited number of plants during the end of April and part of May but observed birds also showed a high preference for this flowering species nectar.

2.5.2 Why don't bellbirds feed on barberry?

Bellbirds were never observed in direct filming observations, Chapter 3, feeding on barberry plants. No faecal samples, Chapter 4, were collected from bellbirds with barberry seeds in them. This evidence strongly supports the previous conclusion that bellbirds were not feeding on barberry fruit. Since barberry is common, eaten by other

birds, and within the size range bellbirds can swallow, this leads to the question of why don't they feed on it?

Comparative studies have suggested that fruit and plant traits, fruit size, colour, spatial subdivision, nutritional composition of fruit pulp and fruit damage, can influence frugivore fruit choice (Fischer and Chapman, 1993, Stiles, 1980, Moermond and Denslow, 1985).

One major fruit trait that can influence frugivore foraging behaviour is gape size and limitations (Wheelwright, 1985, Pratt and Stiles, 1985). Gape limitations are important limiting factor for many frugivorous birds species, if the fruit is too large a bird is unable to swallow it (Wheelwright, 1985, Pratt and Stiles, 1985). New Zealand frugivores have been observed having a slight bias towards smaller fruit of 4–5 mm diameter (Lord et al., 2002). Bellbirds with an average gape size could eat at least 57% of barberry fruit. Even the largest barberry fruit was still smaller than the biggest bellbird gape size. Barberry fruit was within an accessible size range for birds to feed on. Even silvereyes with a small mean gapes of 5.7 ± 0.001 mm were observed in Chapter 3 and 4 selecting and feeding on particular barberry fruit. Gape limitations were not expected to affect the ability of bellbirds to feed on barberry.

Fruit colour is also known to influence foraging behaviour (Wilson et al., 1999, Bach and Kelly, 2004). Most fruiting plants indicate fruit maturity through colour change. This helps stop predation of unripe fruit and helps increase dispersal. Birds can respond to even very subtle colour signals. *Peraxilla tetrapetala* fruit are green at maturity with a small dark ring, yet bellbirds are able to tell the difference between ripe and unripe fruit (Kelly et al., 2004). Ripe barberry fruit is a black/purple colour with a white bloom, un-ripe fruit is a light green this is a substantial colour change that would likely be easily distinguishable. Although red coloured fruit make up 35% of coloured indigenous fruit species in New Zealand, purple/black fruiting plants are the second most common forming 25% of coloured fruiting species (Lord et al., 2002). Therefore barberry fruit colour is not unique within our native forest and it is expected that bellbirds should be able to recognise when it is ripe and available.

Spatial niche separation can influence foraging behaviour. An organism may be capable of feeding on a resource however it is unlikely to if it is outside its spatial niche (Zaret and Rand, 1971, Hutchinson, 1957, Hardin, 1960). Thus bird species that occupy the upper forest canopy are unlikely to feed on the ground floor because of increased competition with the understory niche holders. Observations from

O'Donnell and Dilks (1994) and this study suggested that bellbirds typical foraging microhabitat is the upper to mid-lower canopy levels in forests. Barberry was a mid-level shrub in Kowhai Bush thus bellbirds were often observed feeding in areas that barberry fruit was present and accessible. Further, bellbirds were observed feeding on barberry flowers during spring. It is very unlikely that spatial niche separation and the position of barberry in the forest will play any part in bellbirds decision not to feed on barberry.

The nutritional composition of fruit pulp also influences selection of fruits by birds (Stiles, 1993). Fruit pulp is a natural store of energy which is offered to reward their mutualist dispersers, it is presented in several forms mainly as sugars, lipids or protein (Gautier-Hion et al., 1985). However the sugars, lipids or protein content and composition in fruiting plants varies widely between species (Lotz and Schondube, 2006, Gautier-Hion et al., 1985). Many plant species often either offer a sugar-rich flesh with little fibre, or an aril rich in lipid and protein (Gautier-Hion et al., 1985).

Sugars are a common nutritional reward that fruit offer, they are normally found in three basic forms as either sucrose, glucose, or fructose (Lotz and Schondube, 2006). However birds' ability to assimilate the different sugar types varies between the bird species (Lotz and Schondube, 2006). Honey eaters, Meliphagid, which include bellbirds can assimilate all three of these sugars effectively (Schondube and Del Rio, 2003), between 98-100 % of ingested sucrose can be assimilate by honey eaters (Lotz and Schondube, 2006). However although many of bird species can assimilate each of these three sugars effectively different species have shown a marked preference for one form of sugar over the other (Lotz and Schondube, 2006).

Lipids which are also commonly found in fleshy fruit are high-energy compounds and yield approximately twice the energy on catabolism as either carbohydrates or proteins (Paine, 1971). Similar to sugar levels in fruit lipid levels are highly variable between different plant species (Stiles, 1993). Birds appear to select high-lipid fruits first, when choices of fruits are available (Stiles, 1993). However lipids have a diverse array of chemicals and many birds differ in their ability to assimilate them (Stiles, 1993). Therefore lipids are likely also important factors in birds selection of fruit (Stiles, 1993).

In this study no laboratory analysis was performed to see what sugar or lipid type or compositions were present in barberry fruit. It is possible that barberry plants were offering a nutritional composition that was unappealing to bellbirds and other plants

may have been offering a more appealing nutritional reward. This could mean that the energetic reward from barberry is lower than the native surrounding vegetation and it is therefore less beneficial for the birds to feed on it.

Fruit damage can also play a major role in fruit choice by frigivores. Fruigivors will often avoid areas were fruit is badly damaged (Manzur and Courtney, 1984). During the experiments low rainfall did affect many fruiting plants where fruit was aborted from the main plant. However only <2.7 % of fruit was ever recorded damaged on barberry plants. This is a relatively small percentage of fruit that was damaged so it is unlikely that birds would have entirely avoided plants because of this.

It is likely that differences in fruit selection are related to many nutritional and morphological factors acting in concert and no single character will completely explain bellbirds fruit preference. Fruit offered by barberry was low preference in comparison to other native fruiting species *C. robusta*. The most likely explination is that barberry offers lower quality resources, sugar levels, lipids and minerals, than the native vegetation, simply resulting in barberry becoming a low preference resource.

2.5.3 Effects of barberry on territory size

Under the marginal value theorem an optimally foraging animal exploits resources distributed in patches and must decide when to leave a patch to start searching for a fresh one (Charnov, 2006). Therefore if the resource patches are changed an animal should modify its foraging behaviour to optimally resume resources intake (Charnov, 2006). If barberry had been acting as a resource for bellbirds it is expected that they would likely increase their territory size to gain more resources. Several of the observed bellbirds did change the position of their territories however there was no significant site by time interaction between control and test bird territory sizes after the removal of barberry. Therefore barberry had no effect on bellbird territory sizes.

2.5.4 Future effect barberry could have on bellbirds, and conservation implications

My results suggest that, at least in the short term, the removal of barberry and its fruit is unlikely to affect bellbird behaviour. However if barberry were to remain in Kowhai Bush I speculate that its continued expansion could potentially negative effect

bellbirds. This is because it could reduce habitat quality and available food for bellbirds by out competing native fruiting plants that bellbirds feed on.

Although very few studies have observed the effects barberry has on native vegetation in New Zealand it has been suggested that it may be able to regenerate beneath scrubland forests and compete with native vegetation (Williams and Timmins, 1990, Sullivan et al., 2007). A study carried out by Williams (2011) found that native seedlings can establish and grow beneath barberry canopy. If native vegetation can establish in the understory of barberry it could eventually replace the introduced shrub through succession growth. This is commonly observed with gorse (*Ulex europaeus*), an invasive weed, where native vegetation establish in its understory and eventually through successional growth replaces gorse stands (Williams, 2011). However Williams (2011) study did not observe the long term growth and establishment rates of native vegetation under barberry stands so whether native vegetation can replace the non-native species through successional growth remains to be seen.

Kowhai Bush is made up of large kanuka stands which create a semi shaded environment which can inhibit the establishment of non-shade tolerant plant species (Harris et al., 2004). There was no published literature on barberry shade tolerances however and it was observed successfully establishing through Kowhai Bush's understory. It is therefore likely that it has some shade tolerance and will not be inhibited by Kanuka stand shading. Further it has been observed successionally competing with and replacing gorse and other shrub land species (Sullivan et al., 2007).

Observations in Chapter 3 indicated that on average between 0.34 to 4.45 % of fruit per plant was removed daily and dispersed throughout Kowhai. Dispersal was slow but was happening, Chapter 3 and 4, and there are a lot of fruit per hectare. Although native seedlings have been observed establishing in barberry dominated stands it is possible that the shaded kanuka environment in combination with large barberry stands will increase competition for light, space and nutrients for native shrubs. This could hinder the establishment and growth of native shrubs, eventually reducing habitat and food quality for endemic bellbirds if barberry outcompetes native fruiting shrubs before it is shaded out.

Therefore it is plausible that barberry plants could potentially create inferior habitat for bellbirds within Kowhai Bush. If this occurs it could have negative secondary effects for the bellbirds.

2.5.5 Conclusion

Barberry fruit did not serve as a resource for bellbird for reasons that are currently not known. If barberry was to be removed from areas bellbirds inhabit, the loss of barberry fruit as a resource would probably be positive for bellbirds.

The effect introduced fruiting plants have on both native frugivores and fruiting plants is an inadequately researched field. With the ever increasing number of plants being introduced and eventually naturalising within New Zealand's native ecosystems it is important to understand how introduced plants will affect both our native frugivores and native plants in the future. Future research should focus on the long term effects that introduced fruiting vegetation has within native ecosystems.

Chapter 3

What birds are feeding on barberry fruit?

3.1 Abstract

To find out the dispersal vectors for the invasive weed species barberry (*Berberis glaucocarpa*), video cameras were set up to film 24 barberry plants in Kowhai Bush. Plants were filmed for a total of 242 hours; from this a total of 101 foraging events were recorded including 4 different bird species: silvereyes (*Zosterops lateralis*) 42 visits, blackbirds (*Turdus merula*) 27 visits, song thrush (*Turdus philomelos*) 29, and starlings (*Sturnus vulgaris*) 3 visits. There were considerable differences between these four bird species in relation to visitation, time spent on plants and fruit removal rates. There was a strong correlation between how long birds remain on plants and the number of fruit they removed. Therefore, using total time of visits by each bird is a reasonable estimate of their contribution to fruit removal. Most importantly bird species differed in the mean overall seconds per 1000 fruit per hour they spent on plants which likely reflected the the number of fruit they removed. So the overall contribution to barberry fruit removal during the filming was 32.6% silvereyes, 24.3% blackbirds, 42.9% song thrush and 0.1% starlings. Removal rates for ripe barberry fruit were relatively low (about 0.34 to 4.45 % per day). Further research is needed to understand how barberry will affect native flora and fauna in Kowhai Bush.

3.2 Introduction

Understanding plant invasions is an important and emerging field in ecology, much focus has been placed on understanding the mutualistic bonds that invasive plants form with organisms in their new environment in order to propagate and disperse successfully (Richardson et al., 2000, Reinhart and Callaway, 2006). In particular, many invasive plants species rely on frugivory, the dispersal of seeds via the

consumption of fleshy fruits by frugivores, in order to disperse (Debussche and Isenmann, 1989, Amico and Aizen, 2000, Couvreur et al., 2005, Tabarelli and Peres, 2002, Pakeman et al., 1998).

To survive, invasive fruit dispersal-dependent plants need a positive mutualistic relationship with a suitable frugivore (Buckley et al., 2006). However, fruiting plants introduced into a novel environment often lose their native dispersal agents (Theoharides and Dukes, 2007, Richardson et al., 2000). This can limit their dispersal and in some situations place introduced plants at a disadvantage relative to native species in disperser preference and fruit dispersal rates (Theoharides and Dukes, 2007, Richardson et al., 2000). On the other hand, most avian frugivore dispersal regimes are very generalist and feed on many different fruiting species including a range of novel ones (Renne et al., 2002, Fleming et al., 1993). This allows plants possessing generalized dispersal syndromes to invade novel habitats (Renne et al., 2002). Much of New Zealand's frugivorous avian fauna display generalist foraging strategies (Thorsen et al., 2011); this potentially means that New Zealand is more susceptible to invasion by endozoochoric plants.

It has been proposed by Rejmánek (1996) that the presence of an efficient bird-disperser is also a key predictor for the potential success of a fleshy-fruited invasive species. In New Zealand many introduced plant species including fleshy fruited species have become naturalised within native forests, yet only a small proportion of these have been studied (Vitousek et al., 1996, Callaway and Aschehoug, 2000, Mack et al., 2000). With the ever increasing numbers of plants being introduced and eventually naturalising within native forests, an understanding of bird-mediated seed dispersal is therefore important for both modelling and managing fruiting weed invasions (Overton et al., 2004). It has also been proposed that by targeting the dispersers of introduced plants, either by removing them or monopolising their foraging time, the dispersal of invasive agents could be reduced (Gosper et al., 2005, Buckley et al., 2006).

Barberry, *Berberis glaucocarpa*, is a problem weed species which uses birds as dispersal vectors (Timmins and Williams, 1987, Bakker et al., 1996). It is therefore important to know which bird species are feeding on its fruit and how effective they are at dispersing its seeds. The purpose of this study was to investigate if birds were feeding on barberry fruit in a native regenerating forest (Kowhai Bush), and if so, which bird species were most effective dispersers. This information is important to

understand how the dispersal of barberry could affect the native vegetation in the future and how barberry dispersal could be controlled. To investigate these questions, multiple plants were observed over barberry fruiting season and visits by frugivores were recorded. To study these issues several questions were examined:

1. Which bird species feed on barberry fruit?

2. Which bird species removed the largest quantities of fruit per visit?

3. How long did each bird species remain feeding on plants?

4. Which bird species were the most important foragers and subsequently most likely dispersers of barberry seeds?

5. How effective was the dispersal of barberry in Kowhai Bush?

3.3 Methods

3.3.1 Study site

All observations were carried out in Kowhai Bush (173° 37' E, 42° 23' S), a 240 ha regenerating native forest near Kaikoura, refer to Chapter 2 for more information. Video cameras were used to film which bird species visited barberry plants. Filming started on the 24 February 2011 and lasted through till 20 May 2011.

3.3.2 Study species

The invasive plant species used for the observations was barberry (*Berberis glaucocarpa*). Refer to Chapter 2 for a review of barberry, its introduction and spread in New Zealand.

3.3.3 Video observations

To determine the range of bird species visiting and feeding on barberry fruit, video cameras were used to capture foraging events on 24 selected fruiting barberry plants. A number of studies have used video cameras to collect similar data on: wild chillies (*Capsicum spp*) dispersal vectors (Levey et al., 2006, Tewksbury et al., 1999), seed dispersal within tropical foragers (Jayasekara et al., 2007), fruit removal in the

invasive tree (*Aglaia spectabilis)* (Kitamura et al., 2004), fruit selection by frugivores from native and introduced plants (Drummond, 2005), and fruit removal behaviour by frugivorous bats (Dumont, 1999).

All video recordings were made along Kowhai Bush's eastern areas where barberry was most prevalent (Chapter 2, Fig. 2.3). This area is also adjacent to farmland in which barberry is sometimes used as a hedgerow plant (Chapter 2, Fig. 2.3). Observations were made using two Sony DCR-SR68 video cameras. During January 2011 four video recordings of 2 hours each were made on 4 randomly chosen *C. robusta* plants, a similarly-sized plant to barberry that is highly frequented by frugivores in Kowhai Bush, to determine the optimal settings for recording bird visitations to barberry plants once it ripened later in the year. It was decided that a 720 x 480 wide screen SD resolution was optimal to film plants and yet still be able to identify species of birds clearly. The two cameras filmed simultaneously on different plants, increasing the total number of observations that could be collected. Video cameras were set up 3-5 m from plants and on 1.5 m high tripods. Cameras were placed so that the entire plant was visible as well as a margin of 50-100 cm surrounding the plant. This increased my ability to identify visiting birds. As birds could be seen approaching plants, it was often possible to identify bird species from their flight patterns, and to determine the exact time birds landed and left the plant. However, because of the shape of plants, it was not possible to film all the fruit especially that which was positioned on the opposite side of the plant to the camera or obscured by foliage. Cameras were therefore set so that the majority of fruit was visible. This increased the likelihood that when a frugivore landed and fed, the total number of fruit they removed could be recorded. When cameras were filming the observer always remained at least 50+ meters away. This ensured the observer did not disturb birds or modify the foragers' behaviour.

Filming was not performed on days when there was rain or high wind. Filming was split between morning and afternoon observations to control for time of day and because batteries lasted between 7-8 hours before needing recharging. Video cameras set up in the morning filmed from between 6:30 - 7:30 am until 12:35 – 1:00 pm. Afternoon recordings continued from the moment the morning filming stopped on the observed plant. This was between 12:35 – 1:00 pm until filming ended at 5:30 – 7:00 pm. This covered most of the period from sunrise to sunset. The variation in set up times was due to differences in the time it took to set up the two separate cameras and

changes in day light length. If a morning recording was made on a designated day the following day an afternoon recording would be attempted, this was to control for fruit loss over time. However it was sometimes not possible to film the plant the following day due to adverse weather in which case it was filmed within a maximum of 5 days after the first film. The total length of time that the cameras filmed a single plant was called a filming period. The length of time filming periods lasted also changed from March until May due to changes in day length. A total of 30 plants were filmed throughout the study which was 95 days from first plant filmed to last plant filmed, but 6 of these plants could not be used because of adverse weather, camera faults, or limited visibility in the resulting videos. Thus 24 plants were used in the analysis from the 95 day period. This time spanned the period from the onset of barberry fruit first ripening until fruit began to rot or was completely removed from the barberry plants. A total of 242 hours was recorded on the 24 plants, and, on average, each plant was filmed for 610 ± 30 minutes (range 529 to 727 minutes). Film length varied with changes in daylight length: on average during March each plant was filmed for 12 hours, in April 10 hours and May 9 hours.

After the plant had been filmed, I made a series of measurements the following morning, as I did not want to disturb the plant on the day it was filmed. Observations for each plant included: (1) the date on which the plant was filmed; (2) the position of the plant within Kowhai Bush (to ensure the same plant was not filmed twice); and (3) the total number of ripe, unripe and damaged fruit available on that plant. Due to the size and position of many of the plants it was not possible to directly record which fruit were ripe or damaged. Therefore, the same methods that were used in Chapter 2 to record the total fruit available, total ripe fruit and damage fruit on each individual plant was used for this chapter.

Videos were then transferred to an external hard drive for later analysis. Total time that the plant was filmed was first recorded. Video recordings were played back using VLC media player at a speed of 2-3 times normal until a bird was observed moving towards or landing on the plant, at which point the bird was observed at normal speed. When a bird was observed landing on a plant the following observations were collected: (1) the time the bird first landed on the plant; (2) the species of bird; (3) did it remove and swallow fruit; (4) if possible, the total number of fruit it ate; and (5) the time the bird left the plant. The difference between (5) and (1) gave the total time the bird remained on the plant.

3.3.4 Analysis

The software package R 2.13.2 2 (2011-09-30) was used for all statistical analyses. All graphs were created in SPSS.v16-EQUiNOX.

As there were seasonal changes in day length and fruit ripeness (Chapter 2, Fig 2.3) from summer to winter an ANOVA was used to determine if days since observations began was a predictor for daily number of visits a barberry plant would receive. An ANOVA was also used to test if total ripe fruit per plant was a predictor for the number of visits a plant would receive on the day it was filmed.

Generalized Linear Models (GLMs) were run on data sets to determine which explanatory variables had a significant effect. To control for over-dispersion in the data, quasi GLMs were used with the more conservative "F" test on data sets. Plants were included as a block effect in most GLM analysis to control for variability. Quasi-poisson GLM was used to see if the number of visitations made by birds to plants during a filming period were different between the bird species. Plants were not used as a block effect when the number of fruit removed per visit by each of the bird species was analysed. This was because it was not possible to accurately count how much fruit were removed during each of the bird visits to the plants therefore plants would not act as an effective block effect. A quasi-poisson GLM was used to see if there was a significant difference between the numbers of fruit each species removed per visit. I was always able to record how long each individual bird remained feeding (seconds) on a plant. However qqnorm plots showed that the data for times seconds bird remained feeding on plants was non-normal, therefore data was log transformed to create normality. The log transformed times bird remained feeding on plants was statistically analysed with a gaussian GLM.

When it was possible to record how much fruit a bird removed per visit, the total time the bird remained on the plant was recorded in conjunction with that observation. An ANOVA was then used to determine if the time that birds remained feeding on plants was a predictor for the total fruits removed per visit.

From the raw data it was possible to calculate the average visitation rate to each plant (across all hours of video on that plant) by each bird species, after allowing for plant size and the duration of videotapes, as seconds of bird visit per 1000 fruit per hour. These data are continuous rather than poisson or binomial, but a qqnorm plot showed that the data were non-normal. I then tried log-transforming (x + 1) but

further qqnorm plots showed that it was still highly non-normal, because 68% of all data points were zeros. Therefore the analysis was split into two separate parts. For the first part, a data table was created so that a binomial GLM could be used on the presence or absence of visits to each plant by each bird species (i.e. zero versus non-zero). This tested if the proportion of all plants visited varied among bird species. A new variable was created which for each of the 24 plants had either a 1 if that bird species visited that plant, or 0 if that bird species did not feed on the plant (so n = 96). Secondly, for the cases where some visits were recorded (i.e. excluding the zeros, so n = 31) a Gaussian GLM was used on the log-transformed seconds/1000 fruit/hour to see if there was a difference in visitation rate given that birds were present. These visitation rate data were normally distributed after log transformation, making use of the Gaussian GLM appropriate. Finally, the combined effect of these two factors affecting visitation rate was estimated by multiplying the two together (i.e. proportion of plants visited by bird A times seconds/1000 fruit/hour when bird A went to a plant = overall seconds/1000 fruit/hour by bird A across all plants).

3.4 Results

On average each filmed plant offered a mean of 1170 ± 202 ripe fruit (range 106 to 4013 fruit). A total of 101 bird foraging observations were recorded. In all cases, I was able to identify the species of each visiting bird. A total of four different bird species were observed removing fruit from barberry plants: silvereye (*Zosterops lateralis*), blackbird (*Turdus merula*), song thrush (T. *philomelos*) and starling (*Sturnus vulgaris*) (Table 3.1). Only the silvereye is considered native although it only colonised New Zealand around 1856 (Heather and Robertson, 1998). The other three species were introduced to New Zealand between 1862 and 1883 by acclimatisation societies (Heather and Robertson, 1998). Endemic birds were never once observed feeding on barberry plants. Although some plants offered larger quantities of ripe fruit than other plants, the total available fruit per plant was not a significant predictor for total visitations it would receive per filming period (Table 3.2). Overall there was a significant difference between the numbers of visits a plant would receive from the different species per filming period (Table 3.3).

Although there was a higher percentage of ripe fruit at the end of the fruiting season than at the start (Chapter 2, Fig. 2.1), days since the onset of barberry fruiting was not a significant predictor for the number of visits a plant would receive during a filming

period (Table 3.4). Birds visited plants at similar rates at the start of the season as they did at the end of barberry fruiting season.

There was a significant difference between the bird species in relation to the number of fruit that they removed per bird visit (Table 3.5). This was most likely due to starlings which removed more fruit per individual visit to a plant than blackbirds, silvereyes and song thrushes (Table 3.1). On average silvereyes removed the least fruit per individual visit, followed by blackbirds and song thrush which both consumed similar amounts (Table 3.1). When all visits were considered together the average number of fruit removed per individual visit was 4 ± 0.54 (range 1 to 12 fruit removed). Each plant was visited during each filming period by an average of 4 ± 0.86 birds (range 1 to 16 visits). It was estimated that on average between 2 and 26 fruit were removed from each plant per day. Overall this meant that only between 0.34 to 4.45 % of fruit was removed from each plant per day.

Birds were readily observed landing and leaving the plants, this made it possible to time how long each bird remained feeding on the plants (Table 3.1). There was a significant difference between the four species in relation to how long each species remained feeding on the plants (Table 3.6). Blackbirds remained feeding for the longest time of the four species on average (Table 3.1). They were followed by starlings, while song thrushes and silvereyes remained for the shortest time period (Table 3.1). When all visits were grouped together, birds on average remained on the plants for 47 ± 5.54 seconds (range 1 to 493 seconds).

There was a significant correlation between the total time birds remained feeding on barberry plants and the total number of fruit they ate (Figure 3.1, Table 3.7). In other words, the greater the time a bird remained on the plant the more likely it was to remove more fruit. Therefore, using total time of visits by each bird is a reasonable estimate of their contribution to fruit removal.

There was a significant difference between the bird species in the proportion of plants they visited (Table 3.8), this was most likely due to starlings which were visiting far less plants than the other bird species (Table 3.1). However there was no significant difference between the species in relation to the seconds of visit per 1000 fruit per hour on plants that had visits (Table 3.9), despite wide variation in the means (Table 3.1). This was likely due to the low number of observations and high variance between these observations. When these two variables were combined to work out the overall seconds of visit per 1000 fruit per hour (Table 3.1), song thrush had the

highest overall time and contributed to 42.9% of fruit removal. They were followed by silvereyes who contributed to 32.6% of fruit removal (Table 3.1). Blackbirds contributed to 24.3% of removal (Table 3.1). Lastly starlings had very low overall time seconds per visit per 1000 fruit and contributed to only 0.1% of fruit removal (Table 3.1).

Table 3.1, Visitation rates to barberry fruit by four different bird species in 242 hours of videos on 24 plants.

Bird species	**Silvereye**	**Blackbird**	**Song thrush**	**Starling**
Total number of visits	42	27	29	3
Average fruit removed per visit and (± SE)	1.4 ± 0.24	3.5 ± 0.88	3.6 ± 0.84	9.3 ± 0.63
Average time individual birds remained on the plant per visit (seconds) and (± SE)	31.5 ± 2.6	81.2 ± 24.5	42.4 ± 5.9	44.3 ± 11.5
Total time birds were observed on videoed plants (seconds)	1240	1765	1272	69
Proportion of plants visited by each bird species	0.46	0.37	0.42	0.08
Seconds per visit per 1000 fruit hour (if bird present)	8.62	7.98	12.4	0.29
Overall seconds from visits per 1000 fruit per hour	3.96	2.95	5.2	0.02

Table 3.2 ANOVA output table used to test if total ripe fruit per plant was a predictor for the number of visits a plant would receive from birds during a filming period

Total available fruit on the plants as a predictor for visitations					
Analysis of Variance Table					
Response: Visits to plants					
Model	**d.f.**	**SS**	**MS**	**F**	***P***
Available fruit	1	35.21	35.21	2.08	0.162
Residuals	22	370.75	16.85		

Table 3.3, Quasi-poisson GLM test for testing differences between bird species total visitations to barberry plants per filming period. Plants were included as a block effect in the analysis.

Quasi-poisson species total visitations to barberry plants per filming period					
Model	**d.f.**	**Deviance**	**F**	**Pr(>F)**	**% Explained**
Plants	23	102.6	2.63	**0.001**	37.6
Bird species	3	41.6	8.16	**<0.001**	15.3
Residual	69	127.50			

Table 3.4, ANOVA output table testing if days since observations began was a predictor for visits a barberry plant would receive per filming period.

Days since observations began as a predictor for visitations					
Analysis of Variance Table					
Response: visits to plants					
Model	**d.f.**	**SS**	**MS**	**F**	***P***
Days	1	41.35	41.34	2.48	0.13
Residuals	22	349.61	16.64		

Table 3.5, Quasi-poisson GLM output for testing differences between the numbers of fruit each bird species removed per individual bird visit.

Quasi poisson fruit removed per visit from barberry plants					
Model	**d.f.**	**Deviance**	**F**	**Pr(>F)**	**% Explained**
Bird species	3	34.0	5.04	**0.005**	32.00
Residual	34	72.2			

Table 3.6, Gaussian GLM output table for the log transformed data testing for differences between the bird species for duration seconds of individual visits to plants. Plants were included as a block effect in the analysis.

Gaussian logged time spent on plants by birds				
Model	**d.f.**	**Deviance**	**P(>|Chi|)**	**% Explained**
Bird species	5	25.55	**0.023**	13.7
Plants	17	24.99	0.753	13.4
Residual	69	135.45		

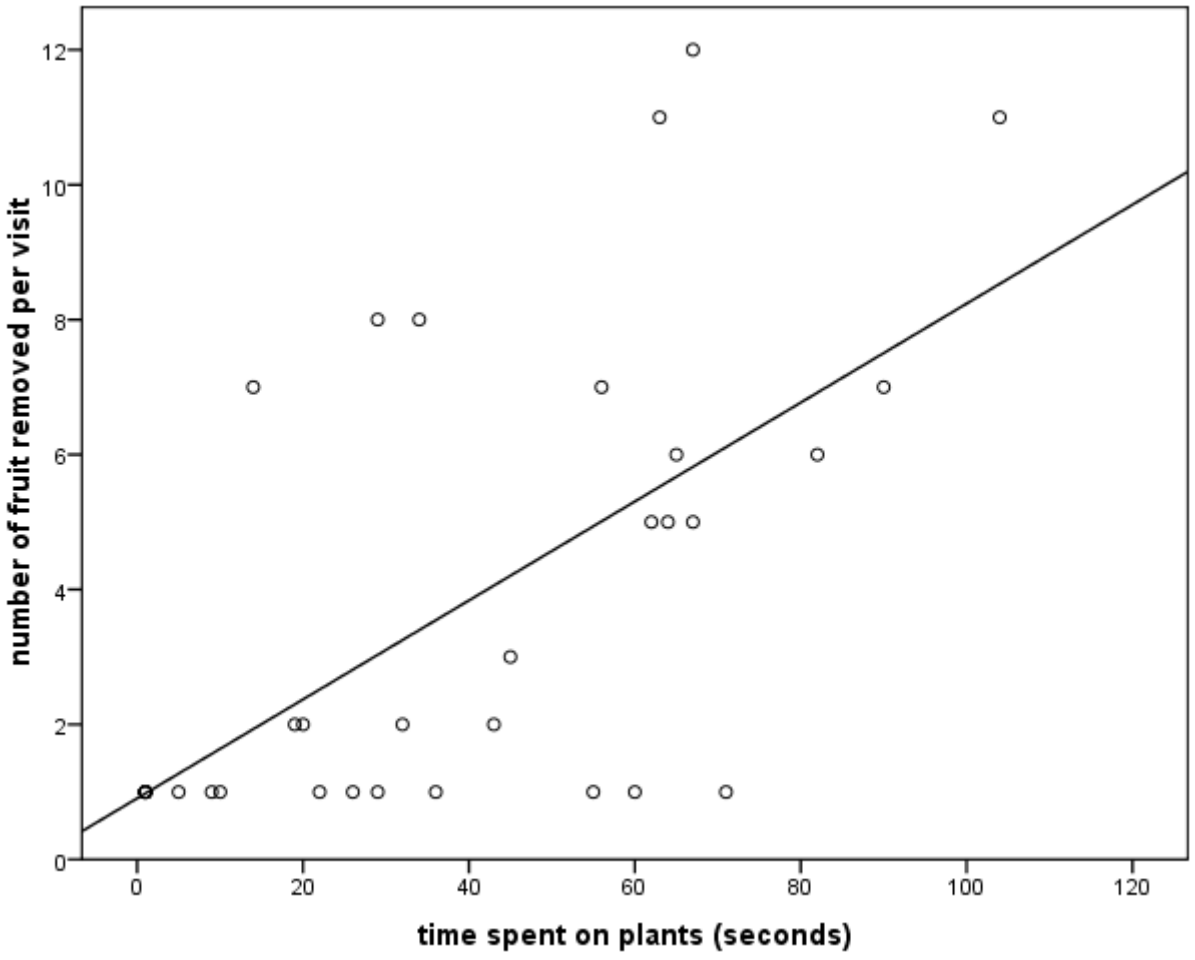

Figure 3.1, Plot for total time seconds per bird visitation vs the total number of fruit removed per bird visit, y= 0.98+ 0.073x.

Table 3.7, ANOVA statistical output testing to see if time, seconds per visit, birds remained on barberry plants was a significant predictor for the number of fruit that would be removed.

Time spent on plants and fruit removed					
Analysis of Variance table					
Response: seeds removed					
Model	**d.f.**	**SS**	**MS**	**F**	***P***
Time	1	159.53	159.53	22.23	**<0.001**
Residuals	33	236.87	7.178		

Table 3.8, Quasi-binomial GLM statistical output testing whether the proportion of plants visited by each bird species was different between the bird species. Plants were included as a block effect in the analysis

Model: quasibinomial, link: logit					
Model	**d.f.**	**Deviance**	**F**	**Pr(>F)**	**% Explained**
Bird species	3	10.98	3.48	**0.019**	8.98
Plants	1	0.273	0.26	0.61	0.22
Residual	91	110.95			

Table 3.9, Gaussian GLM testing to see if the log transformed visitation rate to *Berberis* plants (in seconds of visit per 1000 fruit per hour) was different between the bird species. Plants were included as a block effect in the analysis.

Model: gaussian, link: identity log transformed				
Model	**d.f.**	**Deviance**	**P(>|Chi|)**	**% Explained**
Bird species	3	3.68	0.55	5.8
Plants	17	42.07	0.12	66.3
Residual	10	17.72		

3.5 Discussion

Consumption of barberry was restricted to one self introduced and three introduced dispersal vectors, all of which have arrived either by natural or human intervention into New Zealand over the past 150 years. These were native silvereyes, introduced blackbirds, song thrush and starlings. Only three of these bird species (silvereyes, blackbirds and song thrush) were considered major dispersal vectors. Although starlings visited the plants they overall only acted as minor dispersal vectors. There were significant differences between some species in relation to visitation rates or fruit removal rates. This was generally attributed to starlings which although they removed on average more fruit than their counterparts per visit they had far fewer visitations to fruiting plants and subsequently spent overall a very short time feeding on the plants. In contrast, silvereyes spent less time on the plants than the three introduced bird species per individual visit. Overall seconds of visit per 1000 fruit per hour showed that song thrush were likely the most important dispersers. They were followed by silvereyes. Blackbirds had the third lowest overall time of visit per 1000 fruit per hour. Lastly starlings acted as overall poor visitors per 1000 fruit per hour

From the observations it was estimated that only between 0.34 to 4.45 % of fruit was consumed daily on each individual plant. This represented a low but steady number of seeds dispersed into Kowhai Bush. Similarly, birds only remained on the plants for a relatively short time thus it was likely that the seeds were also effectively dispersed away from the adult plants. If seeds are dispersed to suitable areas, consumption by the four species of birds is likely to increase the fitness of barberry plants, at least relative to seeds that remain in situ and have to compete against the parent plant and other siblings. Therefore it appears, despite being introduced and no longer sympatric with its natural dispersers, that barberry is not dispersal limited by a lack of frugivores. This has many important implications for both predicting the spread of barberry and effects on environmental resistance.

3.5.1 How effective is the dispersal of barberry into Kowhai Bush?

When introduced fruiting plants colonise a new habitat they often lose their native dispersal vectors, this can inhibit their further spread. As a result, most introduced fruiting plants must rely on native or endemic dispersal vectors found within the new novel environment. However, introduced barberry was largely ignored by endemic seed dispersers in Kowhai Bush (Chapter 2). The area has a number of native species

that are known to consume fruit, such as bellbirds (*Anthornis melanura*), South Island robins (*Petroica australis*) and occasionally even fantails (*Rhipidura fuliginosa*), yet none of these were observed feeding on barberry fruits.

However fruit removal and dispersal of barberry into Kowhai Bush was low but steady, due to four other dispersal vectors. Only between 0.34 to 4.45 % of fruit was consumed daily on each individual plant. The size of fruit crops was not a predictor for how many visits a plant would receive per day. Therefore it is expected that as fruit availability changes throughout barberry fruiting season there would not be a change in the mean numbers of fruit removed. This would mean that a plant with 1000 fruit would likely take frugivores between a minimum of 22 and maximum 294 days to remove all available fruit. During this study after 95 days observation period fruit was becoming overripe and beginning to rot it is therefore unlikely that fruit on the plants would last much longer than 100+ days. As plants might take up to 294 days before all the fruit is removed it is likely that many plants were not having all of their fruit removed by the frugivores. However records were never made to see how much fruit was removed by the end of barberry fruiting season. In comparison some plant species such as figs with a crop of ca 100,000 figs could be exhausted in as little time as five days (Jordano, 1983).

Yet there are other factors that could limit barberries expansion and dispersal though Kowhai Bush. The clearest fruit–frugivore relationship is that between fruit size and frugivore gape size (Jordano, 1995). Silvereyes were the smallest common frugivorous bird species observed in Kowhai Bush. Their gape size is smaller than the mean diameter of most barberry fruit (Chapter 4, Figure 4.3). This could inhibit their ability to feed effectively on barberry fruit. Yet, they were observed successfully feeding on barberry fruit (i.e., handling, processing and swallowing fruit). In a few rare instances silvereyes were observed directly or from the video observations forcing fruit into their gape by either pecking or pressing the fruit against the branch. A review by Kelly et al (2010) show that although birds gape size might be smaller than the mean fruit size they can eat whole fruits larger than their measured gape size. Bellbirds with a gape of 5.1 mm were observed excreting seeds of fruits up to 9.7 mm mean diameter and blackbirds with a gape of 9.7 mm excreted seeds of *Alectryon excelsus* (mean fruit diameter 13.0 mm) (Kelly et al., 2010). Silvereyes have been similarly observed excreting seeds of *Prumnopitys taxifolia* (mean fruit diameter 9.5 mm) and hawthorn (mean fruit diameter 9.9 mm, 1.9 times their observed gape of 5.1

mm) (Kelly et al., 2010). Blackbirds, song thrushes and starlings all had gape sizes that could easily accommodate even the largest barberry fruit (see Chapter 4, Figure 4.3 for blackbird and song thrush gape sizes, starlings gape size in Kelly et al (2010) observations was 9.8 mm and lists all other species). Gape limitations are unlikely to play a major part in limiting barberry dispersal.

The major components of disperser effectiveness were discussed in a review by Schupp (1993), of which effective dispersal has both quantitative and qualitative components. The quantity of seed dispersal depends on the number of visits made to the plant by a disperser and the number of seeds dispersed per visit (Schupp, 1993). The quality of seed dispersal depends on the quality of treatment given to a seed in the mouth and gut as well as the quality of seed deposition site as determined by the probability that a deposited seed will survive and become an adult (Schupp, 1993).

The quantity of seed dispersal depended on a range of factors including the frequency of removed fruit. Each barberry plant had a relatively low frequency of visits, on average only 4 a day. Per bird visit only 4 ± 0.54 fruit were removed per plant. Each barberry propagule contains 3.7 seeds (Williams et al., 2000), therefore only a small number of seeds are being dispersed daily per plant. Therefore the overall quantity of seed dispersed was relatively poor for barberry plants.

However quality also needs to be considered, this involves seed dispersal depended on handling, gut passage time and seed deposition. The longer a disperser remains in a plant the more likely seeds are to be deposited under or near the parental plants (Pratt and Stiles, 1983). There are clear advantages to local seed dispersal, > 20 m by large birds, for trees (Schupp et al., 2010). Seedlings that germinate under parental plants likely have higher predations, will have to compete with both the parental plants and siblings as they grow (Schupp et al., 2010). Birds that visited barberry remained on the plants for only 47 seconds on average and the maximum time was 493 seconds. In blackbirds, gut passage time is normally 30 minutes (Sorensen, 1981, Barnea et al., 1991), silvereyes between 22-29 minutes (Stanley and Lill, 2002) and starlings 18 minutes (Levey and Karasov, 1994), song thrush were unknown but likely to be similar times, before defecation occurs. Therefore it is unlikely that seeds would be defecated under or near the parental plants and barberry seeds were likely effectively dispersed away from the adult plant. In Chapter 4 barberry seeds collected from three of the bird species faecal sample were found whole and undamaged 100% of the time.

Habitat selections and dispersal events are also important for quality of seed deposition (Schupp, 1993). Blackbirds and song thrush are ideal species for moving exotic species from cultivated land into native forests (Williams, 2006). It is likely that this is how barberry first entered Kowhai Bush. A limited number of studies have looked at how far each of the observed bird species likely disperses seeds. If observations of blackbirds and seed dispersal events are applied to barberry, it is likely that dispersal events of 50-100 m occur and thus will allow barberry to continue its invasion Kowhai Bush (Davis and Thompson, 2000). Rare gap crossing dispersal events are also likely to create invasive loci up to 2 km away from the parental plant populations (Davis and Thompson, 2000). Overall birds were acting as effective dispersers for the quality of seeds dispersed.

Thus when factors from Schupp (1993) are considered, birds observed in this study are not considered the most effective dispersers for overall quantity of barberry seeds dispersed. However observations would suggest that they were likely effective dispersers for the overall quality of seeds. As barberry fruiting season lasted from mid-February until mid-June, the daily dispersal of seeds over this time represented a sizable seed rain fall per hectare.

3.5.2 Ecological implications

It is likely there will be continued if not increased dispersal and expansion of barberry into Kowhai bush in the future. Therefore it is important to make predictions about how it could potentially influence environmental integrity.

Increasing the number of dispersal vectors available to an introduced plant increases its invasive potential (Stansbury and Vivian-Smith, 2003). This can reduce the environmental resistance native or regenerating forests have against the invasive species. Although barberry did not have a very large dispersal group these species were acting as slow but effective dispersers. It is expected that this will reduce environmental resistance Kowhai Bush has against barberry enough to allow barberry to continue spreading throughout Kowhai Bush.

Work from Sargent (1990) suggests that fruit concentrations in areas surrounding a plant can influence fruit removal rates “neighbourhood effect”. Thus disperser mediated plant fitness is affected by neighbouring plants, whereby with increased densities of the same species during fruiting events enhances overall fruit removal rates rather than inhibiting them (Sargent, 1990). Barberry has only recently become

established in Kowhai Bush therefore its stands are relatively small. If Sargent's (1990) assumptions are correct it could be assumed that as barberry densities increase there will be increased visitation rates to plants. In theory this could create a positive feedback loop between disperser and plant, whereby birds will increase the number seeds dispersed and over time these new thicker stands will further grow and promote increased visitations and dispersal. This has been observed with Hawthorn *(Crataegus monogyna)* in Porters Pass, New Zealand. It was observed that maturing hawthorn trees provided additional food and nesting sites for blackbirds (Williams et al., 2010). Thus the increase in disperser numbers and available fruit from maturing plants lead to increased dispersal of hawthorn and promoted its invasion into Porters Pass (Williams et al., 2010). In Victoria, Austrailia, Blackbird facilitated the expansion of many serious environmental weeds including *Chrysanthemoides monilifera*, *Ligustrum lucidum*, *Myrsiphyllum asparagoides*, *Pyracantha coccinea* and *Schinus molle* through native forests which intern produce more fruit for blackbirds (Carr, 1993).

It is likely that barberry has the potential to negatively affect native biota. Barberry has been observed successionally replacing scrub species (Sullivan et al., 2007). Although some scrub land species such as gorse are considered invasive weeds, native seedlings can still grow and eventually replace gorse stands (Lee et al., 1986), however very little is known about native plants ability to survive and grow under barberry stands (Williams and Timmins, 1990, Sullivan et al., 2007). If barberry encroachment continues into Kowhai Bush it may compete with other native shrubs such as many *Coprosma* species for resources. This could reduce habitat quality and eventually food availability for endemic frugivorous bird species (Chapter 2). However further research is needed to confirm this.

3.5.3 Conservation application

Mature barberry plants are hardy and although it would be easy to spray adult plants with herbicide adult barberry plants often do not die or saplings re-grow from the root systems (ECAN, 2009). Herbicides can also be detrimental to the surrounding native vegetation in forests. To effectively remove barberry seedlings can be carefully pulled out (ECAN, 2009). Other methods include cutting the stump as close to the ground as possible and painting with an appropriate herbicide, or drilling a series of 10 mm holes in the trunk and filling these with glyphosate herbicide, ringbarking and painting

herbicide on the cuts or cutting down and removing the whole tree (AgroSciences, 2012, ECAN, 2009).

However previous studies have suggested alternative methods to control the invasion of fleshy fruited weeds, by targeting the main dispersal vectors of an introduced plant during its fruiting seasons can reduce the dispersal of the weed (Buckley et al, 2006, Gosper et al, 2005). This form of control can potentially save both resources and money. Moody and Mark (1988) demonstrated the importance of controlling isolated populations of invasive plants by reducing their rate of spread. Thus the proposition of manipulating disperser behaviour to reduce dispersal has received support (Wenny, 2001). Gosper et al. (2005) suggested several possible options that can be used to mitigate the dispersal of seeds by manipulating disperser behaviour. These include 1; removing frugivores 2; offering frugivores alternative foods sources 3; making fruit unpalatable for foragers on the targeted invasive species 4; create seed sinks, areas that are inhospitable for seed or seedling survival after they have been deposited there by a forager.

The first option to remove forgivers is unlikely as there were very high abundances of all four of these species and one of them is a native frugivorous species that many native plants rely on for dispersal services. Further these species are also important dispersers for many other fruiting species in Kowhai Bush (Chapter 4). This is not a viable option.

Offering rewards that will monopolise and reduce the time that birds spend feeding on barberry would be more achievable. However, again this could have negative implication for native vegetation. Finding alternative food sources that would monopolise birds' foraging time and related costs could further make this option improbable.

Option three would be the most feasible option whereby fruit are made unpalatable or unappealing for frugivores. Research has demonstrated that frugivores avoid areas where fruit is unappealing potentially because of microbial infections or general damage to the fruit (Manzur and Courtney, 1984, Buchholz and Levey, 1990, Greig-Smith, 1986). If barberry fruit was made unpalatable it is likely that birds would decrease their visitation rates to fruiting plants. This could be achieved by spraying fruit with a foul tasting substance to deter fruit removal. Since barberry is accessible and only found along Kowhai Bush's eastern areas this is a potentially the most feasible option.

The fourth option is more complex than the previous three. Barberry has a high tolerance for a range of conditions. It is unlikely that there would be areas in Kowhai that could act as natural seed sinks. Seed sinks would most likely need to be created artificially which would be highly expensive. Further increased understanding of frugivore behaviour and habitat preferences would also be needed. As very little is known about the foraging behaviour of these four observed bird species in native forests and where they would likely proffer to deposit seeds.

Reducing dispersal of an invasive weed could work but it is unlikely to in this situation with barberry as there is to larger disperser assemblage which is also important for native vegetation. However if barberry had relied on a single disperser which was not important or was also a pest species and it was feasible to reduce the density of this disperser several of these options might have been applicable. Yet this is not the case with barberry and conventional methods of removing plants by hand or using pesticides would be recommended.

3.5.4 Conclusion

Four different bird species fed on barberry fruit. This was split between 3 major dispersers and 1 minor disperser. It is expected that all of these bird species were acting as effective dispersal agents. Although fruit removal was low it was steady and it is expected that future propagation of barberry will increase fruit availability for these frugivores species. If these assumptions are correct a positive feed back loop may occur between barberry and their dispersers which will further enhance the spread of barberry. This could negatively affect native plant and vertebrate species by reducing habitat quality in Kowhai Bush. However, as little is known about barberry and the behaviour of its dispersers, the outcomes are not entirely predictable.

If conservation options were put in place to mitigate barberry dispersal several options were considered by targeting the dispersers. However it is unlikely that these options would work and traditional methods of removing it by hand and painting the roots with herbicide would be more affective at limiting it spread through Kowhai Bush.

Chapter 4

Seed dispersal by native and introduced bird species in Kowhai Bush

4.1 Abstract

Chapter 4 was designed to investigate overall dispersal dynamics within Kowhai Bush, particularly to find out how important exotic birds were for dispersing native and exotic fruit in Kowhai Bush during autumn, March until May 2011. During this time 21 plant species were observed fruiting. I mist netted birds, catching 221 and collected faecal samples to identify the seeds the birds had eaten. A total of 144 faecal samples were collected from six different bird species. From these a total of 1092 seed were identified from 11 different plant species. Another 3 plant species were observed being fed on by birds. This left 7 fruiting plant species with no observed dispersal vectors. There were likely four main dispersers, bellbirds (*Anthornis melanura*), silvereyes (*Zosterops lateralis*), song thrush (*Turdus philomelos*) and blackbirds (*Turdus merula*) and five minor, brown creeper (*Mohoua novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*), fantails (*Rhipidura fuliginosa*), dunnock (*Prunella modularis*) and starlings (*Sturnus vulgaris*) acted as dispersal agents in Kowhai Bush. However there was considerable variability between these bird species dispersal abilities. Introduced birds' song thrush and blackbirds were observed dispersing naturalized plant seeds at higher than expected rates in comparison to native frugivores bellbirds and silvereyes. I also measured the gape sizes on mist netted birds and on samples of fruit from Kowhai Bush. Both silvereyes and bellbirds were found to be eating fruit larger than their gape, but despite this two native (*Hedycarya arborea* and *Ripogonum scandens*) and three exotic plants (*Vitis vinifera, Taxus baccata* and *Crataegus monogyna*) had large fruit that were probably mainly dispersed by song thrush and blackbirds. Rarefaction curves were made for both the total seeds dispersed and the total native seeds dispersed by bird species in Kowhai Bush. This showed that silvereyes had the largest breadth. They were followed by song thrush and black birds which were expected to have increased breadth with

increased samples. Lastly were bellbirds. However when only native vegetation was observed blackbirds mean diet breadth dropped below bellbirds mean diet breadth. This Chapter shows that exotic birds are important frugivores in regenerating native forest, for dispersing large fleshy fruited native seeds at sites where some native birds (tui, kereru) are rare or absent. However this comes at a trade of to the increased number of weed species seeds they disperse. Hence, the interactions among native and exotic fruit and frugivores are complex, and important for the future composition of forest communities.

4.2 Introduction

Frugivorous birds historically and presently perform the vast majority of fruit dispersal services in New Zealand forests (Thorsen et al., 2009, Thorsen et al., 2011, Lee et al., 1991, Clout and Hay, 1989). However, over the past 1000 years BP a number of native dispersal vectors have become extinct in New Zealand (Thorsen et al., 2011). Many surviving frugiovores species have suffered population declines or localised extinctions (O'Donnell, 1996, Atkinson, 1973, Diamond and Veitch, 1981, Heather and Robertson, 1998). For example, bellbirds (*Anthornis melanura*) are now absent from part of their historic range in Northland (Heather and Robertson, 1998). Similarly, the range of the North Island kokako (*Callaeas cinerea wilsoni*) has been vastly reduced due to predation from introduced stoats (*Mustela erminea*), possums (*Trichosurus vulpecula*) and rats (*Rattus* spp.) while the South Island kokako (*C. c. cinerea*) has become extinct (Clout and Hay, 1989). These species are considered key dispersal agents, and kokako may once have been almost as important as endemic kereru (*Hemiphaga novaeseelandiae*) in relation to the number of fruiting species they feed on, however their limited ability to fly may have reduced their dispersal efficiency (Clout and Hay, 1989). As a consequence, New Zealand was described by Diamond (1984) as no longer having an avifauna, just the wreckage of one.

These extinctions or declines likely reduced dispersal efficiency, especially for plants with large seeds (Williams and Karl, 1996, Clout and Hay, 1989). In contrast to the loss of native frugivores, over the past 150 years many foreign bird species been introduced into New Zealand (Green, 1997, Heather and Robertson, 1998). Despite their variety, introduced bird species are no longer considered important seed dispersers in comparison to native seed dispersers within native forests (Kelly et al., 2010, Kelly et al., 2006). Introduced birds have been observed to feed on and disperse

introduced fruiting plants at higher rates than native and endemic bird species within native forests (Williams and Karl, 1996). Dispersal of adventive weeds into regenerating scrub by introduced birds is one of the most common detrimental mechanism affecting our indigenous forests (Timmins and Williams, 1987). Thus frugivore-mediated dispersal of invasive plants has become an area of emerging importance in the weed management sector, highlighting a need for information on how frugivores, and in particular, invasive frugivorous birds are affecting weed population dynamics and spread.

The role of birds in the dispersal of native and introduced plants is especially important for the management of remaining lowland native forests, which are often highly fragmented and reduced in area. For example, Kowhai Bush is one of the largest remaining lowland fragments of native forest in the Kaikoura area but a noticeable absence from this forest is the kereru (*Hemiphaga novaeseelandiae*), which is an important disperser of large native fruits >15 mm (Kelly et al., 2010). Tui (*Prosthemadera novaeseelandiae*) visit Kowhai Bush during summer but at very low numbers. Endemic bellbirds and native silvereyes (*Zosterops lateralis*) are present and are the only native fruit dispersers to remain year round and at high numbers in Kowhai Bush. In contrast to the paucity of native birds, several species of introduced bird including blackbirds (*Turdus merula*), song thrush (*Turdus philomelos*), dunnocks (*Prunella modularis*), starlings (*Sturnus vulgaris*) and several finch species; chaffinch (*Fringilla coelebs*), redpoll (*Carduelis flammea*), greenfinch (*Carduelis chloris*), goldfinch (*Carduelis carduelis*) and yellowhammer (*Emberiza citrinella*) occur in Kowhai Bush throughout the year. Similarly there are a number of naturalized plant species that are now classified as weeds in Kowhai Bush (Howell and Sawyer, 2006, Howell, 2008). This combination of a diverse disperser assemblage and the presence of a variety of introduced and native fruiting species makes Kowhai Bush an interesting area to study dispersal dynamics of both native and introduced fruiting plants by both native and introduced bird vectors. It is also a regenerating native forest and thus it is important to understand the dispersal processes that are occurring within it.

In this Chapter, my objective was to observe dispersal dynamics within the regenerating native forest of Kowhai Bush. Specifically, I examined:

1) Which plant species were fruiting in Kowhai Bush over autumn?

2) Which plant species were birds feeding on (from both direct observations and faecal samples), and of these, which species did the birds deposit seeds?

3) To what extent did bird gape size limit the species of fruit they fed on?

From these observations, I determined which bird species were dispersing which plant seeds, and whether they were dispersing these seeds at higher or lower than expected rates. Comparisons were also made between bird species to see which were dispersing adventive seeds at higher or lower than expected rates. The overall food web between the observed frugivores and dispersed seeds was detailed to map the dispersal dynamics and the strength of these interactions within Kowhai Bush. Comparisons were made between the bird species and I used rarefaction curves to compare the observed diet breadth of each bird species. This gave a representation of the dispersal dynamics of each bird species and allowed me to assess which species were effective native seed dispersers.

4.3 Methods

4.3.1 Study site

All observations were carried out at Kowhai Bush, a 240 ha regenerating native woodland near Kaikoura (173° 37' E, 42° 23' S). Refer to Chapter 2 (2.2 methods, 2.2.1 study site) for more information. The composition of the vegetation of Kowhai Bush is given by Hunt and Gill (1979).

4.3.2 Mist netting operations

Data were collected by catching birds in mist nets and then collecting faecal samples which contained seed. The collected seed samples were used to determine the identity of the plants that birds were feeding on. Similarly, mist-netted birds were used to measure gape size. Mist netting was conducted through autumn, from 1 March until 31 May 2011, when yearly fruit abundance is at its highest. Mist netting was not carried out on days with adverse weather such as rainy or overly windy days. Nets were erected on average 16-20 days each month and were placed in forest margins, clearings, or beneath the forest canopy. Days when netting occurred were split

between morning and afternoon periods. Morning netting occurred from 0730 until 1300 h and afternoon netting from 1300 until 1730 h. Nets with 38 mm mesh were suspended between self-supporting poles 3.3 m tall. A combination of four nets were used at any one time; these were two 6 m long and two 12 m long nets. Nets were taken down each night but the support poles were left in place. This meant that nets could be rapidly set up each morning or afternoon increasing the total catch time. Nets were checked every 10-15 minutes to remove entangled birds. Nets were only set up in one area for a maximum of 5 days before being moved a minimum of 50 m away. This increased variation in habitat types, increased the chances of catching different individuals within a species, and reduced the likelihood that birds became wary of the nets.

To increase catch rates, audio and visual decoys were used to lure birds into the nets. Bellbird alarms and calls were played back between 1 to 2 hours during each netting period. When bellbird alarm calls were used a stuffed predator (cat) was also used as a visual stimulation at the same time. Bellbirds that arrived would often also alarm call when they observed the cat which would attract other bellbirds to the nets. Blackbirds and song thrush were attracted with audio playbacks of conspecific birdsong, which was also used between 1-2 hours each netting period. A stuffed bird of the same species was used as a visual stimulus. Audio playbacks of silvereye song were also used to lure silvereyes into the net for 1-2 hours.

Plastic sheets 1 m wide were placed under each of the nets. When birds became entangled in the net they normally defecated on to these sheets. Faecal samples were then collected off the sheets and the bird species was noted. Netted birds were untangled within minutes, but if they had not defecated onto the plastic sheet they were placed in a paper or cloth bag for 5-10 minutes. If they did not defecate after this it was unlikely they would; thus, standard body measurements were then collected and they were released. For each individual captured, I recorded its sex, age, species, weight and gape size (see Hulsman (1980) and Boyle (1983) for gape and other measurement methods). Birds were banded before release to comply with Department of Conservation regulations. Bellbirds were also colour banded to help with other research (Chapter 2). After a faecal sample was collected it was stored in 70% alcohol before being examined under a dissecting microscope. Observed seeds were then identified to plant species. All whole fruit or seeds were identified with the aid of a

reference collection created by collecting fruit from Kowhai Bush during the observational period.

4.3.3 Direct feeding observations and fruit availability

Direct observations of fruit were made to determine which fruiting species were available to the frugivores. Throughout autumn, I also made a series of casual observations on a non-systematic basis of foraging birds to determine if they fed on other plant species that were not observed in their faecal samples. If a bird was observed feeding on fruit, both the identity of the bird and the plant species was recorded along with date.

Methods for measuring fruiting periods and fruit availability are based on Williams and Karl (1996). Observations were made at least three times a month on the abundance and ripeness of fruit from the same 5-10 plants from each species. The plants were located along tracks in the forest and on adjacent land. Results are presented as the period when 5-35%, 36-65%, or 66-100% of the fruit were ripe and available (Table 4.1). Due to an inability to accurately measure the fruit availability two fleshy fruited plant species were not included in table 4.1, *Cordyline australis* and *Pseudowintera colorata*. Abundance of a fleshy-fruiting species was ranked on a 6 point subjective scale, the estimated number of plants that would likely be encountered within 50 x 50 m square was also included: (1) plants not in Kowhai Bush but present within 0.25 km of Kowhai Bush: (2) very uncommon in Kowhai Bush 1-2 plants, (3) uncommon 3-6 plants, (4) patchy 6-10 often clumped together, (5) common 10-15 plants, and (6) abundant 15+ plants. Fruit samples were collected from 5-10 accessible fleshy-fruited individual plants of each species and these were used in the seed reference collection and to measure the diameter of fruit for comparison with the size of gape size. Five to ten ripe fruit were collected from these plants at their period of maximum ripeness. The least diameter, which determines swallowing ability (Kelly et al., 2010), was then measured on 25 fruit from each species to estimate the mean diameter of the fruit and the range. The flesh was then removed before seeds were stored as a reference collection. The mean sizes of four fleshy fruiting species were not measured due a shortage of fresh material for analysis: *Leucopogon fasciculatus, Pseudowintera colorata, Muehlenbeckia australis* and *Cordyline australis*. *Pittosporum* sp. was also not included since they produce a woody seed capsule and not fleshy fruit. These species are not included in figure 4.3.

4.3.4 Analysis

The software package R 2.13.2 (2011-09-30) was used for all statistical analysis. All graphs were created in SPSS.v16-EQUiNOX. Seeds were used as the main unit for the statistical tests and graphs. This was appropriate for this study as the objective was to look at seed dispersal rates by the observed bird species.

To analyse which bird species were dispersing seeds at higher or lower than expected rates a chi square test of independence was used. The aim was to see if the expected and actual seeds deposited were significantly different between the different bird species. If <35 seeds in total were identified in the faecal samples of a bird species it was not used for the statistical analysis. Several of the plant seeds were only found at very low numbers (1-15 seeds per faecal sample) and often in only one of the observed bird species faecal samples. Although Chi square tests can deal with numbers as low as 5 the results were likely inaccurate for these observations. Therefore <35 seeds were used for the statistical outputs for the observations this made the Chi square tests more robust. A relatively low number of observations were collected for two bird species, so it was not possible to analyse the faeces of brown creepers (*Mohoua novaeseelandiae*) and dunnocks. Only bellbirds, silvereyes, song thrush and blackbirds were used in the statistical analysis. Similarly, if <35 seeds were identified for a particular plant species it was not used in the statistical analysis, which left seven plant species able to be analysed in the chi square test: *Pseudopanax arboreus, Coprosma robusta, C. rhamnoides, C. propinqua, Muehlenbeckia australis, Melicytus ramiflorus, and Berberis glaucocarpa*. For the remaining plant species they are only mentioned as observations.

To analyse which bird species were dispersing introduced seeds at higher or lower than expected rates a chi square test of independence was also used. The aim was to determine if bellbirds, silvereyes, blackbirds and song thrush were dispersing either introduced or native seeds at higher or lower than expected rates. Seeds found in each of the bird's faecal samples were classified into the two groups, native or naturalised seeds. A chi squired test was then run to see if there were higher or lower than expected seed numbers in either of the two groups for each of the four bird species faecal samples.

Bipartite networks were used to visualise seed and disperser interactions occurring in Kowhai Bush and the associated strengths between each interaction. Bipartite

networks are commonly used to show plant-pollinator, seed-disperser and parasite-prey interactions (Watts and Strogatz, 1998, Jordano et al., 2003, Bascompte and Jordano, 2007, Dormann et al., 2008). Bipartite networks focus on webs consisting of only two trophic levels (Watts and Strogatz, 1998, Jordano et al., 2003, Bascompte and Jordano, 2007). The Vegan package in the statistical software package R was used to create the bipartite graphs. The link between the bars represents an association between the seed-disperser interactions while the variable thickness of the bars indicates the relative frequency of the interactions.

Rarefaction curves were made for both the total seeds dispersed and the total native seeds dispersed by bird species in Kowhai Bush. The former gave a representation of the total dispersal dynamics and the latter a representation of which birds were effective native seed dispersers. Rarefaction curves have been used to show disperser fruit foraging breath by showing increasing expected number of seed species detected with increasing numbers of faecal samples (Poulsen et al., 2001, Hyatt and Casper, 2000, Heck Jr et al., 1975). Curves were presented with 95% confidence intervals. Rarefaction curves showed the total dietary diversity (the total number of fruit species consumed). Only birds with at least 50 identified seeds from their faecal samples were used in the rarefaction curves. Only 4 bird species were used in the rarefaction curves: bellbirds, silvereyes, song thrush and blackbirds.

4.4 Results

A total of 20 fleshy-fruited and one woody seed capsule plant species were observed fruiting in Kowhai Bush during autumn (Fig. 4.1). Of the 20 fruiting species 4 are naturalised weeds. The number of observed fruiting species changed monthly with 15 plant species fruiting in March, 20 in April and 17 in May (Fig. 4.1). Of these 21 species, only 11 were recorded in faecal samples (Table 4.1). Of the remaining 9 species direct foraging observations were noted on 3 (Table 4.1). This left 7 species with no observed dispersal vectors (Table 4.1).

A total of 221 birds were caught in mist nets from March-May, this sample was comprised of 10 different species (Table 4.2). Relative catch rate gave a poor representation of bird abundance as song thrushes, blackbirds and some large bellbirds could avoid entanglement in mist nets. A total of 183 faecal samples were collected of which only 144 faecal samples contained seeds. A total of 1092 seeds were found in the 144 faecal samples, and all seeds were identified to a likely

corresponding plant species. Seeds were found whole and undamaged 100% of the time.

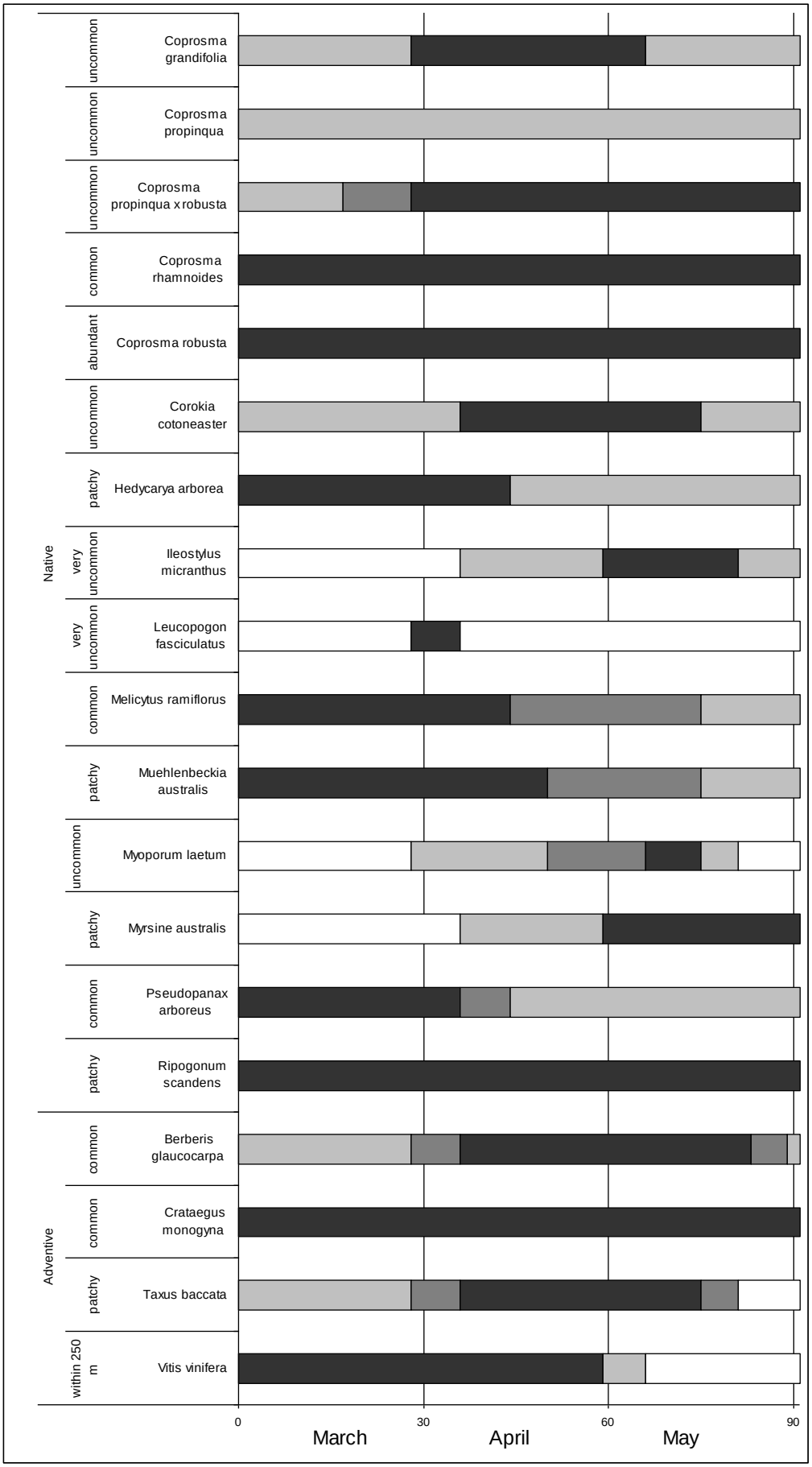

Figure 4.1, Seasonal observations of fruit availability for frugivores at Kowhai Bush. Clear no fruit available or fruit is not ripe, light grey 5-35% fruit ripe, grey 36-65% fruit ripe, dark grey 66-100% of fruit are ripe. Figure is split between native fruiting species and adventive fruiting species that were found in Kowhai Bush. Each plant species is labelled with how common it was throughout Kowhai Bush.

Table 4.1, Summary of all native and naturalised fruiting plants present in Kowhai Bush and recorded as being feed on by birds, either from faeces samples (F) or from observations (O).

	Endemic			Native		Introduced				
Plant species	**Bellbird**	**Brown creeper**	**Tui**	**Silvereye**	**Fantail**	**Blackbird**	**Song thrush**	**Dunnock**	**Starling**	**Total bird species feeding on fruit (n)**
Native species										
Coprosma grandifolia	O	-	-	-	-	-	-	-	-	**1**
Coprosma propinqua	F	-	-	F	-	-	-	-	-	**2**
Coprosma rhamnoides	F	-	-	F	O	-	F	-	-	**4**
Coprosma robusta	F	-	O	F	O	F	F	F	-	**7**
Cordyline australis	-	-	-	-	-	-	-	-	-	**0**
Corokia cotoneaster	-	-	-	-	-	-	-	-	-	**0**
Hedycarya arborea	-	-	-	-	-	-	-	-	-	**0**
Ileostylus micranthus	F	-	-	F	-	-	-	-	-	**2**
Leucopogon fasciolatus	-	-	-	-	-	-	-	-	-	**0**
Melicytus ramiflorus	-	F	-	F	-	-	-	-	-	**2**
Muehlenbeckia australis	F	F	-	F	-	F	-	-	-	**4**
Myoporum laetum	-	-	-	-	-	-	-	-	-	**0**
Myrsine australis	-	-	-	-	-	-	-	-	-	**0**
Pseudopanax arboreus	-	-	-	F	-	F	F	-	O	**4**
Pseudowintera colorata	-	-	-	-	-	-	F	-	-	**1**
Pittosporum sp	-	-	-	F	-	-	-	-	-	**1**
Ripogonum scanden	-	-	-	-	-	-	-	-	-	**0**
Total native spp (n)	**6**	**2**	**1**	**8**	**2**	**3**	**4**	**1**	**1**	
Naturalised species										
Berberis glaucocarpa	-	-	-	F	-	F	F	-	O	**4**
Crataegus monogyna	-	-	-	-	-	O	-	-	-	**1**
Vitis vinifera	-	-	-	-	-	F	O	-	-	**2**
Taxus baccata	-	-	-	-	-	O	O	-	-	**2**
Total naturalised spp				**1**		**4**	**3**		**1**	
Total fruit in birds diet (n)	**6**	**2**	**1**	**9**	**2**	**7**	**7**	**1**	**2**	

Table 4.2, Summary of birds caught and faecal samples collected per bird species. Birds are listed descending from most total seeds identified

	Bird species	Birds caught	Faecal samples collected	Faecal samples with seeds present	Seeds identified from faecal samples	Average seeds per faecal sample
Bird species that deposited seeds	Silvereye	109	94	90	574	6.4
	Bellbird	40	36	36	325	9.0
	Blackbird	15	14	10	134	13.4
	Song thrush	7	7	5	52	10.4
	Dunnock	3	3	1	4	4.0
	Brown creeper	2	2	2	3	1.5
Bird species that did not deposit seeds	Fantail	24	14	-	-	-
	Grey warbler	17	11	-	-	-
	Chaffinch	3	3	-	-	-
	South island robin	1	1	-	-	-
	Total	**221**	**183**	**144**	**1092**	**7.6**

4.4.1 Plant species in bird diets

There was a significant difference between the expected and observed seed species in the faecal samples ($X^2 = 279.3$, df = 18, $P < 0.001$). All four bird species were drivers of this significant difference: bellbird, silvereye, song thrush and blackbird.

The endemic bellbird was one of the main drivers for the significant difference between the bird species deposition rates. *Coprosma robusta* formed the vast bulk of seeds deposited by bellbirds (Table 4.3). Their deposition rates for *C. robusta* were higher than expected, while their deposition rates for *Pseudopanax arboreus* and *Berberis glaucocarpa* were lower than expected (Table 4.4). Overall, they had a relatively narrow diet, feeding on only 6 native plant species and primarily on *C. robusta* (Table 4.1 and 4.3).

Native silvereyes deposited *Melicytus ramiflorus, Pseudopanax arboreus* and *Muehlenbeckia australis* seeds at higher than expected rates (Table 4.4). However, they feed on *C. robusta* at lower than expected rates (Table 4.4). They were also the only bird species observed depositing *Pittosporum* sp seeds. Silvereyes had the highest catch rate and were observed feeding on the largest range of fruiting species (Table 4.1 and 4.3).

Blackbirds were depositing *Pseudopanax arboreus* at lower than expected rates and feeding on *Berberis glaucocarpa* at higher than expected rates (Table 4.4). They were observed feeding on 7 different plant species (Table 4.1).

Song thrushes only deposited *Berberis glaucocarpa* seeds at higher than expected rates (Table 4.3). They were also the only bird species observed depositing native *Pseudowintera colorata* seeds (Table 4.1). Overall, they were observed feeding on 7 different plant species (Table 4.1 and 4.3).

Seed samples were collected at low numbers from endemic brown creepers and introduced dunnocks (Table 4.3).

Endemic tui were rarely encountered during the study and never caught in mist nets. On two occasions birds were observed feeding on *C. robusta* (Table 4.1). Observations were also made of native fantails feeding on *C. robusta* and *C. rhamnoides* fruit on multiple occasions (Table 4.1).

Large flocks of 40-50 starlings were often observed feeding on *Pseudopanax arboreus* trees. On occasion, birds were observed regurgitating seeds that were identified as *Pseudopanax arboreus* (Table 4.1). In Chapter 3, I report on starlings that were observed visiting *Berberis glaucocarpa* fruit in low numbers.

4.4.2 Dispersal of introduced fruit

There was a significant difference between the expected and observed deposition rates of introduced seeds deposited by the four main bird species. ($X^2 = 99.45$, df = 3, $P < 0.001$). Endemic bellbirds and native silvereyes both deposited introduced seeds at lower than expected rates (Table 4.5). Introduced fruit seeds were never observed in the bellbird's diet and only made up 2.3 % of identified seeds in silvereye's faecal samples. Introduced blackbirds and song thrush both deposited introduced fruiting plant seeds at higher than expected rates (Table 4.5, Fig. 4.2). Introduced seeds made up 18.6 % of observed seeds in blackbird faecal samples and 13.5 % of indentified seeds in song thrush faecal samples (Fig. 4.2). There was no significant difference between the expected and actual observed deposition rates for native seeds between the four species.

Table 4.3, Summary of % identified seeds in endemic, native and introduced birds faecal samples from Kowhai Bush.

	Endemic		Native		Introduced	
	Bellbird	**Brown Creeper**	**Silvereye**	**Song thrush**	**Blackbird**	**Dunnock**
Plant species						
Native						
Coprosma robusta	90.4	-	54.2	53.8	80.6	100.0
Coprosma rhamnoides	5.6	-	7.3	1.9	-	-
Coprosma propinqua	1.9	-	5.9	-	-	-
Ileostylus micranthus	1.2	-	0.2	-	-	-
Melicytus ramiflorus	-	33.3	5.2	-	-	-
Muehlenbeckia australis	0.9	66.7	7.5	-	0.7	-
Pittosporum sp	-	-	0.9	-	-	-
Pseudopanax arboreus	-	-	16.6	1.9	-	-
Pseudowintera colorata	-	-	-	28.8	-	-
Total native seeds observed						
%	100.0	100.0	97.7	86.5	81.3	100.0
Naturalised						
Berberis glaucocarpa	-	-	2.3	13.5	13.4	-
Vitis vinifera	-	-	-	-	5.2	-
Total naturalised seeds observed %	0.0	0.0	2.3	13.5	18.7	0.0

Table 4.4, Chi square table of observed and expected numbers of seed deposited by the four bird species, bellbirds, silvereyes, song thrush and blackbirds for 7 observed plant species. The total number of seeds deposited for the 7 plant species by each species is presented at the top.

	Bellbirds N=320		**Silvereyes N=556**		**Song thrush N=37**		**Blackbirds N=128**	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Berberis glaucocarpa	0	11.5	13	20.5	7	1.3	18	4.6
Coprosma propinqua	6	12.2	34	21.6	0	1.4	0	4.9
Coprosma rhamnoides	18	18.5	42	32.9	1	2.1	0	7.4
Coprosma robusta	293	224.9	311	399.2	28	26.0	108	90.0
Melicytus ramiflorus	0	9.1	30	16.2	0	1.1	0	3.6
Muehlenbeckia australis	3	14.3	43	25.4	0	1.7	1	5.7
Pseudopanax arboreus	0	29.5	95	52.3	1	3.4	1	11.8

Table 4.5, Chi square table of observed and expected number of seed deposited by the four bird species, bellbirds, silvereyes, song thrush and blackbirds for native and adventive plant species. The total number of seeds deposited by each species is presented at the top.

	Bellbirds N=324		**Silvereyes N=574**		**Song thrush N=59**		**Blackbirds N=134**	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Native seeds	324.0	310.6	561.0	550.3	52.0	56.6	109.0	128.5
Adventive seeds	0.0	13.4	13.0	23.7	7.0	2.4	25.0	5.5

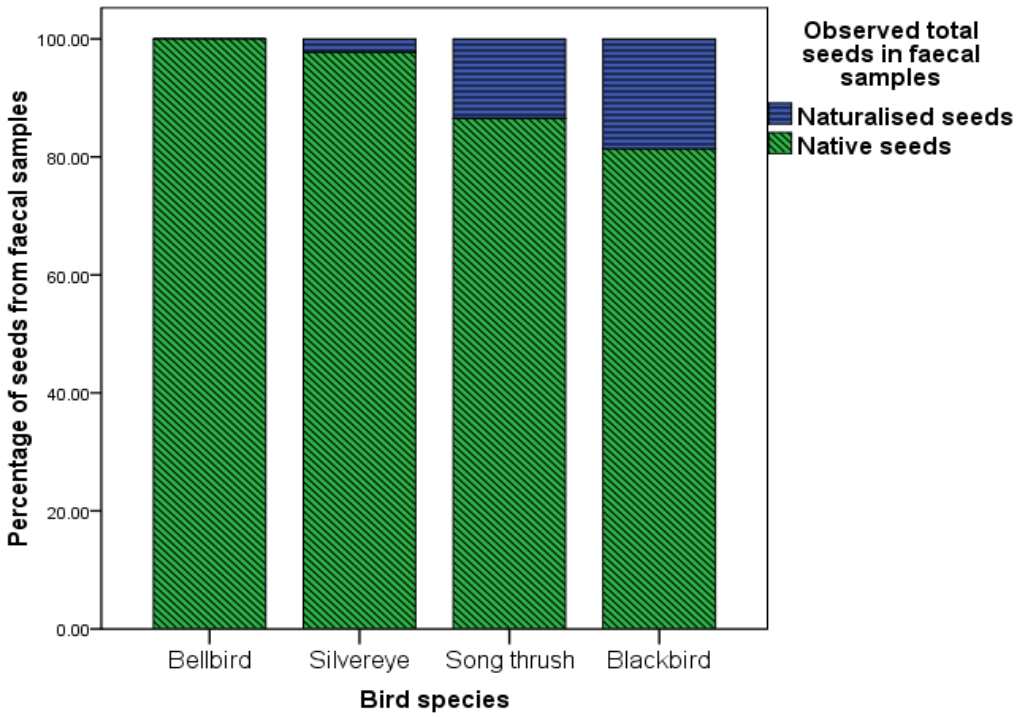

Figure 4.2, Total percentage composition of native or introduced seeds identified in bird species faecal samples.

4.4.3 Gape size and limitations

Fruit size were recorded along with mean bird gape size to determine which fruit a bird species were unlikely to feed on due to gape limitations. Blackbirds had the largest gape size 11.9 ± 0.04 mm, n = 8 (range 11.6 - 12.4 mm, Fig. 4.3). Introduced song thrushes had similar gape sizes to blackbirds but was slightly smaller 11.6 ± 0.24 mm, n = 5 (range 10.9 – 12.3, Fig. 4.3). Observations from mean fruit diameter showed that blackbirds and song thrushes could swallow all the fruiting species in Kowhai Bush and this included native *Hedycarya arborea* and *Ripogonum scandens* fruit (Fig. 4.3). Bellbirds had a relatively smaller gape 7.9 ± 0.01 mm, n = 15 (range 5.6 - 8.8 mm, Fig. 3). Of the 5 largest fruit species in Kowhai Bush they likely struggled to feed on, 3 were introduced and two were native species (Fig. 4.3). Silvereyes had the smallest gape size 5.7 ± 0.001 mm, n = 27 (range 5 - 6.5 mm, Fig. 4.3) and likely only feed on a limited number of fruiting species (Fig. 4.3). However, observations were made of silvereyes feeding on *Berberis glaucocarpa* fruit which would be considered out of their gape range so some allowance should be made for possible fruit and gape size variances.

4.4.4 Food web model

Bipartite interaction seed dispersal webs were created to show community dispersal networks for seeds dispersed by bird species in Kowhai Bush (Fig. 4.4). This was made for the bird species in which faecal samples were collected. There was a mean links per species of 1.59. Overall, there was relatively low specialisation (H2'=0.28) by birds in relation to plant seed dispersal. However, *C. robusta* was observed dominating the observations as it formed 68.2 % of the total seed observations. The second most commonly deposited species was *Pseudopanax arboreus* (8.8 %), whose dispersal was dominated by silvereyes. The third most commonly observed species was *C. rhamnoides* which formed 5.7 % of the deposited seeds and was primarily observed in the diet of bellbirds and silvereyes. The remaining observations of plant seeds were low and only formed a total of 17.5 % of the total seed observations (Fig. 4.4). Silvereyes formed the bulk of bird observations and demonstrated a generalist frequency of interactions (Fig. 4.4). Endemic bellbirds had a very strong frequency of interactions with *C. robusta* which dominated their seed dispersal observations (Fig 4.4). Blackbirds also feed on large quantities of native *C. robsuta,* but they also fed on introduced *Berberis glaucocarpa* and *Vitis vinifera* (Fig 4.4).

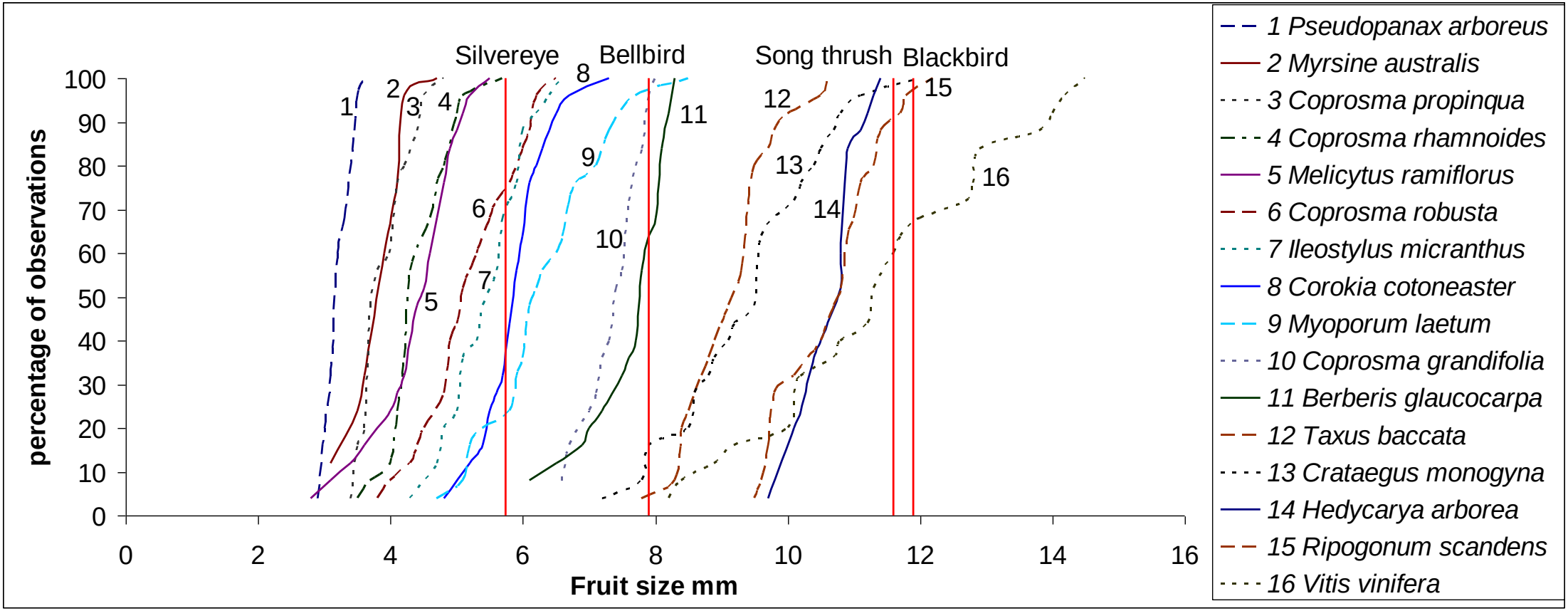

Figure 4.3, A cumulative distributions of fruit diameters for 16 of the fruiting plant species in Kowhai Bush, autumn 2011. Plants are listed from smallest to largest fruit. The mean gape size for silvereye, bellbird, song thrush and blackbird are presented as the straight red lines. The name of each bird species is positioned above their mean gape size.

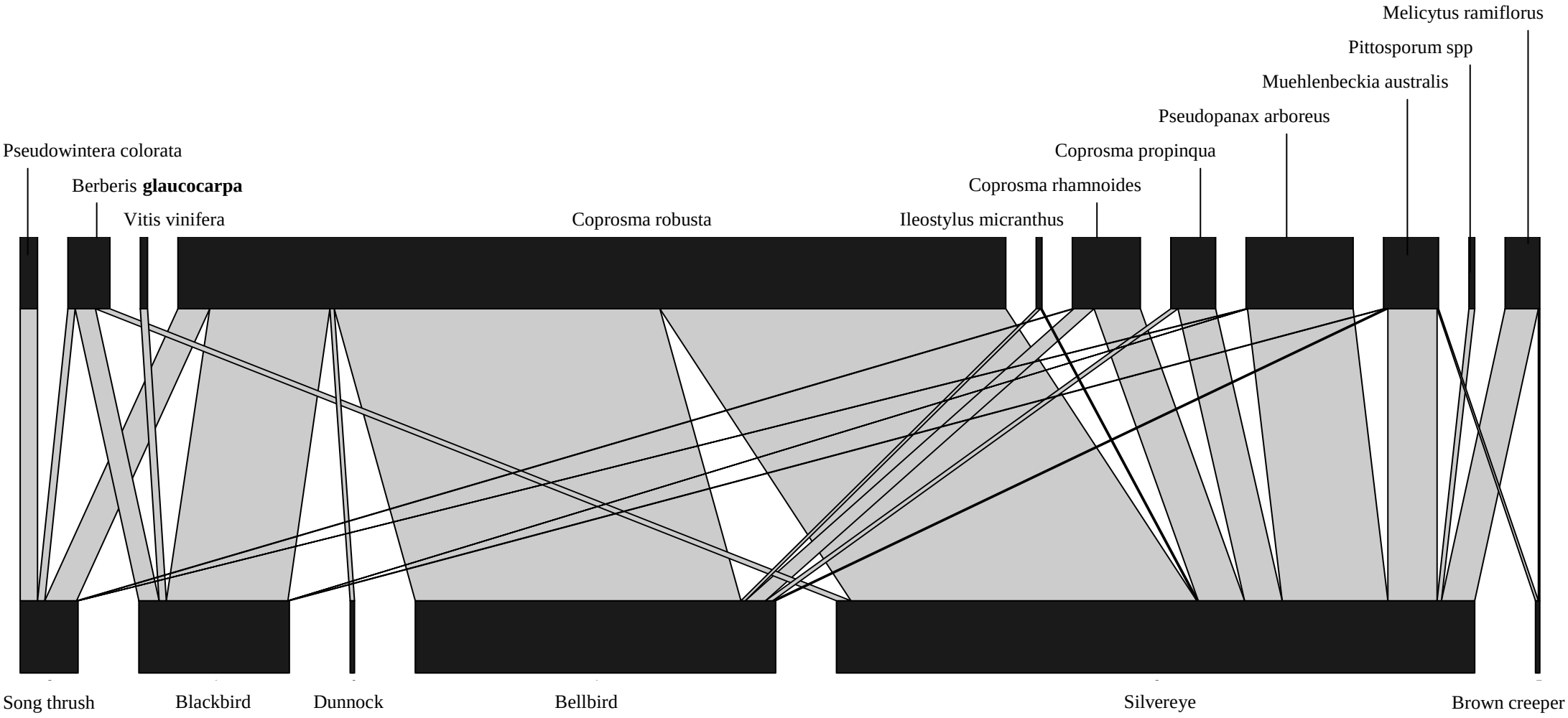

Figure 4.4, bipartite network for the seed dispersers. The link between the bars represents an association between the seed-disperser interactions while the variable thickness of the bars indicates the relative frequency of the interactions. The numbers of seeds indentified in the birds' faecal samples are used as the unit linking frugivores to plant species.

4.4.5 Rarefaction curves and bird diet breadth

Rarefaction curves were calculated to see whether estimates of diet breadth were affected by the number of faecal samples collected. Overall silvereyes dispersed the most plant species within a short number of subsamples (Fig. 4.5a). This showed that they had a large breadth of fruit species in their diet and were predominantly generalists. This was followed by song thrush, in which the observed mean species richness in individual subsamples rapidly increased suggesting that they were also prominent generalist seed dispersers (Fig. 4.5a). Yet, the mean species density curve of song thrushes did not plateau and it is likely they would be found to disperse more plant species with increasing number of samples. Blackbirds mean diet breadth was only slightly below song thrush's breadth, however blackbirds' curve had not begun to plateau and it is likely that they also had a larger seed dispersal breadth with increasing sample size. Bellbirds had a slow increasing slope which suggested that they were more specialized on a few plant species (Fig. 4.5a). Further, they had the lowest mean species breadth over the individual subsamples (Fig. 4.5a). Unlike blackbirds and song thrush, the curve for bellbirds plateaued and it was therefore unlikely that they would be found to have a much greater foraging breadth with increasing numbers of subsamples.

A second rarefaction cure was performed by removing introduced fruits seed from the analysis to allow the assessment of the likely effectiveness of each species for the dispersal of native vegetation (Fig. 4.5b). Overall silvereyes, song thrush and bellbirds remained within similar parameters as the previous rarefaction cure (Fig. 4.5a). Only the blackbird's diet breadth had major changes, dropping below bellbirds diet breadth but still within its confidence interval overlap (Fig. 4.5b). This would suggest that when considering only native seed deposition, blackbirds had a smaller diet breadth for native vegetation than the previous three species and were overall inferior dispersers for native vegetation.

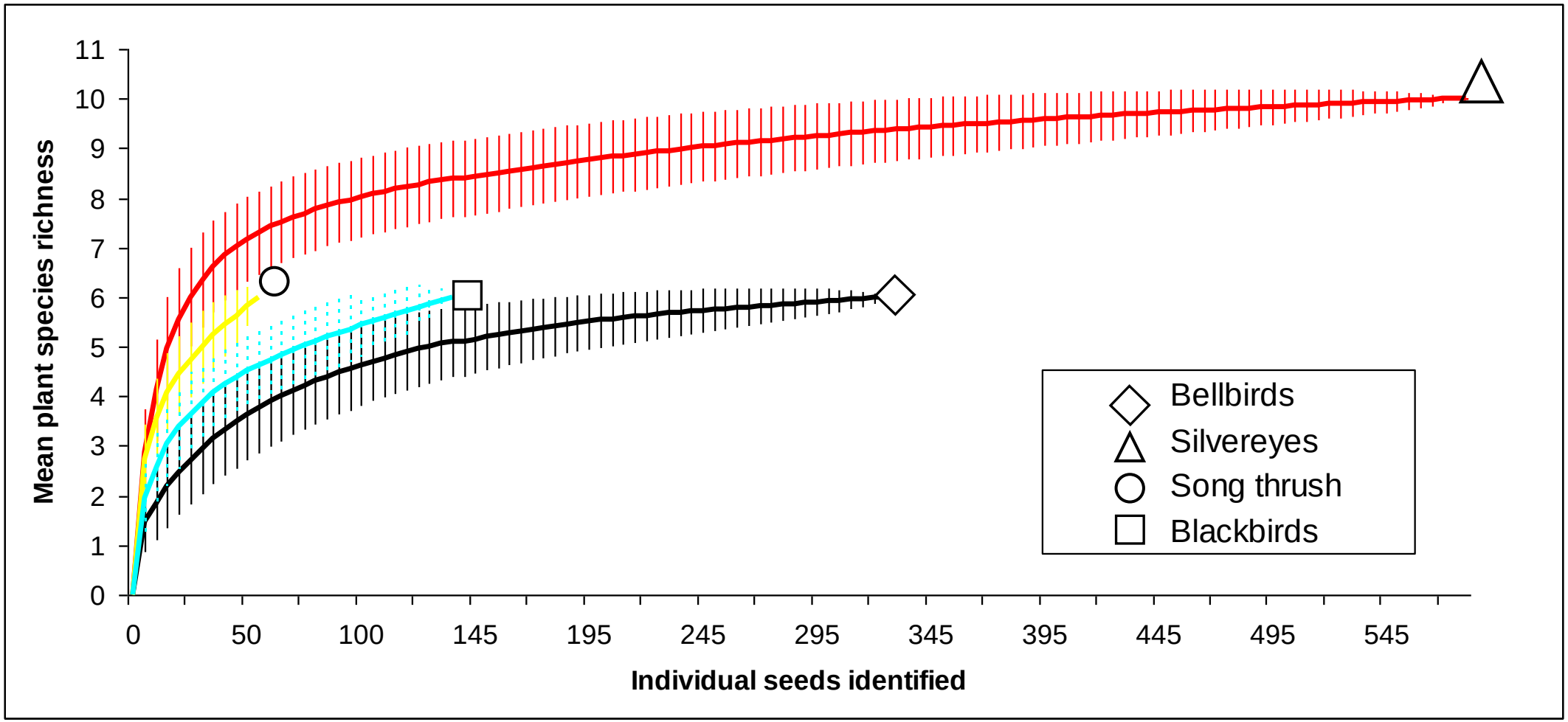

Figure 4.5a, Rarefaction curves of the expected total number of seed species in Kowhai Bush detected with increasing numbers individual seeds identified in faecal samples.

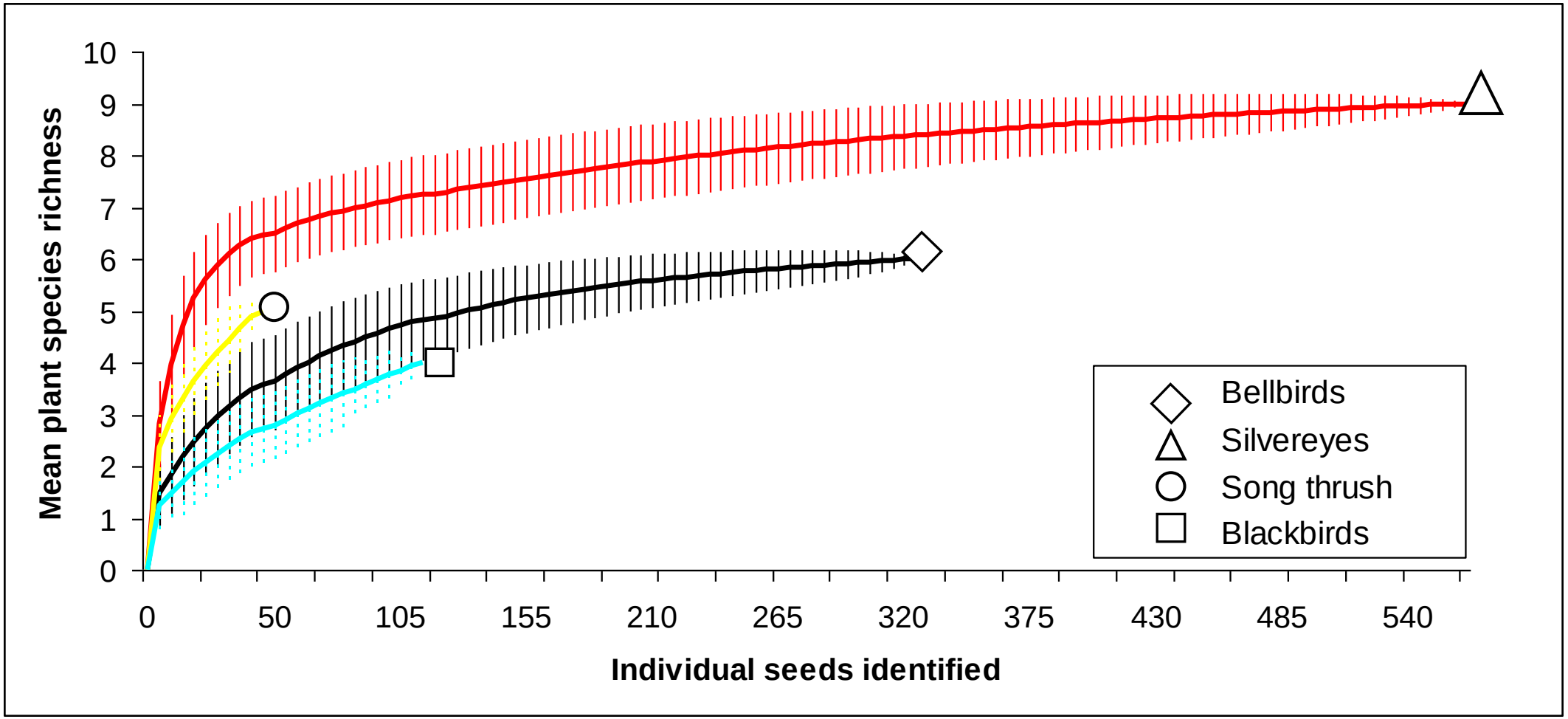

Figure 4.5b, Rarefaction curves of the expected number of native seed species detected with increasing numbers of individual seeds identified in faecal samples.

4.5 Discussion

There was considerable variation between the bird species in relation to seed dispersal. Overall, four species of bird were likely the main dispersal vectors for fruiting plants in Kowhai Bush; endemic bellbirds, native silvereyes, introduced blackbirds and song thrush. Collectively these four species were observed dispersing 14 different plant species, 11 from faecal samples and 3 from direct observations, during autumn. This left 7 fruiting plant species with unobserved dispersal vectors. Of the observed 14 plant species in bird diets 4 of these were introduced species. However, faecal samples were also collected from two minor seed dispersers (brown creepers and dunnocks). Speculations could also be made about tui, fantails and starling dispersal capabilities as these birds were observed visiting fruiting plants in Kowhai. In particular large flocks of starlings were observed feeding in Kowhai Bush.

4.5.1 Fruit foraging and seed dispersal by observed bird species

Bellbirds and tui were the only medium-sized endemic fruigivores observed in Kowhai Bush during autumn. Within bellbirds diets *Coprosma robusta* dominated the seeds they dispersed, a pattern observed previously (Williams and Karl, 1996, O'Donnell and Dilks, 1994). In contrast, bellbirds largely ignored native *Melicytus ramiflorus* and *Pseudopanax arboreus.* While they clearly avoided naturalised fruit, of particular note is that bellbirds avoided foraging on the locally abundant weed *Berberis glaucocarpa* in comparison to the other three main dispersal vectors which did feed on it. Similar observations of bellbirds avoiding adventive fruit have been made in the literature which suggests that bellbirds do not often use adventive fruit as a resource (Allen and Lee, 1992, O'Donnell and Dilks, 1994, Williams and Karl, 1996). In general, bellbirds had a limited diet in comparison to the other three main dispersal vectors.

Tuis were the only other medium endemic frugivore in Kowhai Bush. They were only observed in very low numbers on a seasonal basis, from the start of summer until the start of autumn March-April and had disappeared by May. However, they were observed feeding on *C. robusta*. Fruit is thought to be an important component of the tui diet. For example, O'Donnell and Dilks (1994) observed fruit forming 48% of their diet in April. Thus, it is likely that despite their low numbers they could be dispersing seeds on a regular basis in Kowhai Bush when they were present. This could be

important for some of the larger fruiting species as tui have a large gape (9.7 mm), and it is estimated that they could potentially swollow fruit up to a maximum of 15 mm (Kelly et al., 2010).

Limited seed samples were also collected from the faecal samples of the endemic brown creeper which contained native fruit seeds, *Melicytus ramiflorus* and *Muehlenbeckia australis*. Generally, the brown creeper is considered an insectivorous species (Gill, 1980), however other observations have been made of brown creepers feeding on fruit where it formed 0.5-3% of their diet (O'Donnell and Dilks, 1994).

Native silvereyes had the most diverse diet out of the observed frugivores, feeding on 9 different fruiting species and demonstrated an overall generalist foraging behaviour. Unlike the other main dispersers, silvereyes were observed dispersing *C. robsuta* at lower than expected rates. Furthermore, silvereyes dispersed *Melicytus ramiflorus*, *Pseudopanax arboreus* and *Muehlenbeckia australis* at higher than expected rates compared to the other frugivores. All of the fruit that silvereyes fed on at higher than expected rates are relatively small and easily within silvereyes gape limits. Similar observations have also been made of silvereyes displaying very generalist foraging behaviours in relation to seed dispersal (Williams and Karl, 1996, O'Donnell and Dilks, 1994). These observations, coupled with the high numbers of silvereyes present in Kowhai Bush, would suggest that silvereyes are probably the most important seed dispersers in Kowhai Bush which is consistent with Kelly et al (2006) findings.

Although no faecal samples were collected from fantails with seeds in them they were observed feeding on *C. robusta* and *C. rhamnoides.* Although fruit is not a common part of their diet it has been observed forming 0.3% of their diet in previous studies (O'Donnell and Dilks, 1994).

Introduced song thrush demonstrated interesting trends. Although low numbers of birds were caught sufficient seed samples were collected to suggest that song thrushes are a prominent generalist seed disperser. Observations indicated that they did feed on *Berberis glaucocarpa* at higher than expected levels. They had a high generalist diet breadth and were the only bird species observed feeding on native *Pseudowintera colorata.* Unfortunately, few observations have been made of song thrush foraging behaviour in New Zealand because of their generally secretive behaviour, however they are considered one of the top three most important dispersers for adventive weeds introduced from England to New Zealand (Snow and Snow, 2011). Observations from song thrush would support the idea that introduced birds disperse naturalised species at

higher than expected rates. As song thrush were observed foraging on three of the four naturalised plant species in Kowhai Bush and dispersing their seeds at higher than expected rates. However observations from this study still show that they were still dispersing higher overall quantities of native fruits seeds than naturalised plant species seeds.

Introduced blackbirds had a varied diet but a considerable part of this was comprised of introduced fruit from *Berberis glaucocarpa* and *Vitis vinifera.* Blackbirds also fed on introduced *Berberis glaucocarpa* at higher than expected rates. Similar to song thrushes, blackbirds are considered one of the top dispersers of naturalised fruiting plants introduced into New Zealand (Williams and Karl, 1996). Observations would support this idea as they dispersed larger than expected quantities of introduced seeds and were observed feeding on all of the introduced plant species in Kowhai Bush. Nevertheless, the majority of blackbird diet in Kowhai Bush was comprised of native *C. robusta* which indicates that although they are dispersing introduced fruit they are also dispersing large quantities of native seeds.

Fruit has been observed playing a minor role in the dunnock diets (O'Donnell and Dilks, 1994), however there is no mention in the literature of which fruiting species dunnocks feed on. Observations from this study indicate that they do feed on *C. robusta*.

Starlings were commonly observed in Kowhai Bush in large flocks of 40-50 birds. Unfortunately, starlings never descended into the lower canopy where mist nets were positioned so no samples could be collected. Birds were commonly observed feeding on *Pseudopanax arboreus,* and they were also observed regurgitating seeds. The regurgitation of seeds by native birds in New Zealand is very rare, there are only three recorded instances of regurgitation in New Zealand (Wotton et al., 2008). Starlings in the USA have been observed regurgitating seeds (LaFleur et al., 2009), yet this is likely the first reported instance of starlings regurgitating seeds in New Zealand. When these dropped seeds were examined they were *Pseudopanax arboreus.* In Chapter 3 starlings were also filmed feeding on *Berberis glaucocarpa* along the forest margins.

4.5.2 Fruit preferences native vs naturalised

There was a marked difference between endemic bellbirds, native silvereyes, introduced blackbirds and song thrush in relation to fruit choices. Endemic bellbirds were never once observed feeding on introduced fruit. Complimentary observations were made in Chapter 2. Where bellbirds were directly observed for 52 hours, during

this time they were also never once observed feeding on naturalised fruiting species. These observations are similarly reflected in previous research that indicated that endemic frugivores showed lower preference for adventive fruit (O'Donnell and Dilks, 1994, Williams and Karl, 1996). Similarly, silvereyes showed a preference for native vegetation and dispersed only one naturalised plant species *Berberis glaucocarpa*, which was observed in their faecal samples in low numbers. These observations are reflected in the results which show that both endemic bellbirds and native silvereyes dispersed introduced seeds at lower than expected rates. However, silvereyes do undertake local migrations to urban areas, particularly in autumn and winter and this could increase the dispersal of *Berberis glaucocarpa* from urban to native environments (Kikkawa, 1962).

In contrast to bellbirds and silvereye, introduced song thrushes and blackbirds were the main dispersers of introduced fruit in Kowhai Bush and were dispersing naturalised fruit at higher than expected rates. It is therefore likely that the spread of introduced fruiting species into Kowhai Bush will be primarily performed by these two species. However some consideration should be given to the fact that although introduced birds were dispersing introduced plants at higher than expected rates it was still well below the total percentage of native fruit that introduced birds dispersed. Further, there was no difference between the observed and expected dispersal rates of native fruiting species between the four observed bird species. It is therefore likely that they were having a positive effect on some of the native vegetation by acting as dispersal vectors for these species. From the perspective of endemic and native frugivores, the naturalised weed species studied here represented an inferior food source in that the fruits they bear were largely ignored. Thus, it can be inferred that where adventive fruiting trees and shrubs colonise sites or replace indigenous species, they likely create inferior habitats for these frugivores.

4.5.3 Gape limitations

Large endemic fruguivores, such as the kereru, have large gape sizes and disperse large seeded fleshy fruits were absent from Kowhai Bush. Similarly, tui which have a large gape size were rare in Kowhai Bush. This could result in dispersal limitations for large fleshy-fruited seeds due to gape limitations from the remaining bird species (Wheelwright, 1985, Alcántara and Rey, 2003). Of the observed plant species, five of them are considered too large for both endemic bellbirds and native silvereyes to easily feed on. Only two of these five species were native (*Hedycarya arborea* and

Ripogonum scandens). Yet song thrush and blackbirds had large enough gapes to feed on all available fruiting species effectively. Although both *Hedycarya arborea* and *Ripogonum scandens* were not observed in faecal samples of blackbirds and song thrushes, both have been reported feeding on these two fruiting species in previous literature (Clout and Hay, 1989, Kelly et al., 2010). It has also been suggested that blackbirds are likely to be a principal disperser of large seeds in the absence of native pigeons (Williams, 2006). The distribution and capacity of blackbird to consume large numbers of fruit greater than 7–8 mm diameter place them in a potentially important position as dispersers in a range of habitats (Williams, 2006). Thus dispersal of these two plant species is likely to be performed by introduced bird species in Kowhai Bush.

Three of the four naturalised plant species found in Kowhai Bush had fruit sizes that would also be difficult for endemic bellbirds and native silvereyes to swallow. All three of these plant species were either observed in faecal samples or being feed on by blackbirds and song thrushes. Thus, although blackbirds and song thrushes were potentially acting as distributers of large native seeds they were also dispersing large fleshy fruited introduced species.

Some consideration should be given to the exact size of fruit that birds can swallow. A review by Kelly et al. (2010) showed that many birds can eat whole fruits despite the fruit being larger than the measured mean gape sizes of some bird species. Bellbirds were observed with a gape of 5.1 mm, but excreting seeds of fruits up to 9.7 mm diameter and blackbirds with a gape of 9.7 mm excreted seeds of *Alectryon excelsus* (fruit diameter 13.0 mm) (Kelly et al., 2010). Silvereyes have been similarly observed excreting seeds of *Prumnopitys taxifolia* (mean fruit diameter 9.5 mm) and hawthorn (fruit diameter 9.9 mm, 1.9 times their observed gape 5.1 mm) (Kelly et al., 2010). During this study similar observations were made of silvereyes with a gape of 5.7 mm feeding on barberry fruit with a mean diameter of 7.6 mm. Two factors that might allow birds to eat whole fruits larger than their gape should be considered. Firstly, soft fruit may be malleable and could be forced past a bird's gape (Kelly et al., 2010). In Chapter three, I reported that silvereyes were observed forcing barberry past their gape by placing the fruit in their mouth then pecking the branch they were standing on to force it in. Secondly, variance in gape and fruit sizes, some birds will have larger gape sizes than the mean population size similarly some fruit will be smaller than average size (Kelly et al., 2010). This would mean some birds with larger than average gape sizes could feed on fruit that was smaller than average.

4.5.4 Rarefaction and birds' diet breadth

Rarefaction curves displayed the relative seed dispersal breadths for each of the bird species. Overall, silvereyes had the largest disperser breadth of the four observed species. They demonstrated a very rapid increase in the mean number of species observed in their diets with increasing samples. This suggested that they had a very generalist diet and did not concentrate on only one particular plant species. They were followed by song thrushes. However, due to limitations in this study it was not possible to predict when mean species richness would plateau for this species diet. Their plateau was not reached this suggested that they were likely to have higher mean seed species richness if increased samples were collected. This would place them as very effective seed dispersers in Kowhai Bush. Blackbird's mean dispersal breadth was lower than song thrush and silvereye as they did not feed on such a large range of plant species as these two species. Similarly to song thrushes, the rarefaction curve for blackbirds had not plateaued suggesting that with increasing seed samples they would have a larger seed dispersal breadth than indicated by the current observations. Bellbirds had a relatively small dispersal breadth which indicated that they generally specialized on a few plant species (particularly *C. robusta*). Thus endemic bellbirds were likely acting as inferior community-wide dispersers compared to the three previous frugivores.

As effective seed dispersers for native vegetation, blackbirds were the only species to show any major changes in their rarefaction curve after introduced seeds were removed from the observations in comparison to the other three species. Their dispersal capabilities for native vegetation dropped below that of bellbirds. This would suggest that blackbirds were the least effective community wide disperser for native vegetation. Introduced song thrushes' diet breadth remained higher than that of endemic bellbirds, suggesting that they were acting as a more effective disperser for a range of native plant species than the endemic species in this study.

4.5.5 Plant species that were not observed in birds diets

Seven of the plant species in Kowhai Bush were not observed in bird diets. This did not necessarily mean they were not fed on. In previous studies all 7 of these plant species have been observed in the diets of bird species that occur in Kowhai Bush. Presented is a list of the plant species with their corresponding dispersers that have been observed in previous studies; *Cordyline australis,* silvereyes, starlings, blackbirds (Williams and Karl, 1996, Burrows, 1994), *Ripogonum scandens,* blackbirds and songthrush (Williams and Karl, 1996, Burrows, 1994). *Myrsine australis,* silvereyes,

bellbirds, blackbirds and tui (O'Donnell and Dilks, 1994, Burrows, 1994). *Myoporum laetum,* bellbirds and starling (Ferguson and Drake, 1999, Burrows, 1994). *Hedycarya arborea,* bellbird, blackbirds and song thrush (O'Donnell and Dilks, 1994, Clout and Hay, 1989). *Corokia cotoneaster* blackbirds (Burrows, 1994). *Leucopogon fasciculatus* silvereyes (Williams and Karl, 1996). It is likely that during this study birds would have been feed on these plant species in Kowhai Bush even through no samples or observations were collected. This could have occurred because several of the plant species were uncommon in Kowhai Bush therefore direct observations of the plants were infrequent. Similarly because there were few plants it is expected that they would also be less common in the faecal samples collected from birds.

4.5.6 Introduced birds as replacement dispersers?

Kowhai Bush poses an interesting example in which introduced birds could be more capable of dispersing large fleshy fruited plants over long distances than the current assemblage of native frugivores. In other words, species such as the introduced song thrush appear to be more effective seed dispersers for all sizes of native fruiting vegetation. Due to gape limitations in native birds, and lack of large endemic seed dispersers, it was likely that two native plant species had to rely largely on introduced birds to disperse their seeds over long distances. Similar situations on a larger scale have occurred in the Hawaiian Islands (Foster and Robinson, 2007). The Hawaiian Islands have lost nearly all their native seed dispersers, but have subsequently gained some introduced frugivorous bird species (Foster and Robinson, 2007). This includes; Japanese white-eye (*Zosterops japonicus*), red-billed leiothrix (*Leiothrix lutea*), Japanese bush-warblers (*Cettia diphone*), hwamei (*Garrulax canorus*), northern cardinals (*Cardinalis cardinalis*), spotted doves (*Streptopelia chinensis*), and Indian myna (Foster and Robinson, 2007). Introduced birds have been observed facilitating the dispersal of native fruit throughout both native forests and adventive forests in Hawaii (Foster and Robinson, 2007). Thus the maintenance of many native plant populations now depends on introduced birds in some of Hawaii's native forest (Foster and Robinson, 2007). Although this situation is more extreme than the observations made at Kowhai Bush there are similarities. If song thrushes and blackbirds are dispersing large seeds in Kowhai Bush, the absence of the native kereru (and rarity of tui) may not create a noticeable impact on the large seeded plant populations (Loiselle and Blake, 2002). Although this clearly needs further study, it is likely that introduced birds to an

extent are having a positive effect on the regeneration of large seeded plant species in Kowhai Bush.

Despite any potential benefit to native vegetation, dispersal of seeds by introduced birds in Hawaii had a down-side in that introduced birds were also acting as effective dispersers of introduced fruiting species and facilitating their spread into native forests (Foster and Robinson, 2007). In Kowhai Bush, species that dispersed the most naturalized species seeds where introduced song thrushes and blackbirds. In particular song thrushes and blackbirds were the only bird species dispersing large seeded naturalised plant species. If song thrushes and blackbirds were potentially having a positive effect on the dispersal of native vegetation, it is likely that this comes at a trade off to their ability to disperse introduced vegetation in Kowhai Bush.

4.5.7 Conclusion

Dispersal of fruiting vegetation in Kowhai Bush was most likely performed by four frugivourous bird species; endemic bellbirds, native silvereyes, and introduced blackbirds and song thrushes. Four other species were dispersing some seeds; endemic tui and brown creepers, and introduced starlings and dunnocks. Both brown creepers and dunnocks are likely only minor seed dispersers, while the dispersal capabilities of tui and starlings remain to be studied. There was considerable variation between bird species in relation to which plants they feed on. Silvereyes are likely the most important seed dispersers in Kowhai Bush due to their sheer numbers and diverse fruit diet. Interestingly, song thrushes were also likely to be important seed dispersers as they had the second highest mean fruit species richness in their diets and were possibly dispersing large fleshy fruited seeds in the absence of kereru in Kowhai Bush. However this comes at a price as they also disperse seeds from introduced fruiting species. Similarly blackbirds dispersed a large mean number of species and potentially dispersed large native seeds. However they dispersed the most naturalised species and were considered overall inferior dispersers for native seeds. Bellbirds also acted as relatively poor dispersal agents for overall native fruit species. Although they only feed on native vegetation they primarily just feed on native *C. robusta* which formed 90% of their diet and largely ignored most other native fruiting species. However this might change depending on *C. robusta* fruit available in following years.

Due to the limited kinds of observations made it is hard to be certain which species were the most important dispersers in Kowhai Bush. To accurately predict how much dispersal was occurring, the relative population sizes of these birds would need to be

estimated so that correlations could be made between population size and dispersal characteristics. More focus should also be directed towards introduced birds as potential seed dispersers for native fruiting species. Future research should continue to focus on seed dispersal dynamics within native regenerating forests to more accurately assess the overall roles of each frugivorous species and how this could affect the future composition of native forests.

Chapter 5
General Discussion

The last three Chapters have revealed some novel observations in relation to fruit removal mutualisms and seed dispersal dynamics in a regenerating native forest. Disperser mutualisms, and in particular the effect introduced fruiting vegetation has on frugivores, are inadequately researched topics. Given the large number of exotic plants and animals now established in New Zealand, more research is especially needed to understand dispersal mutulisms and invasive plant - disperser dynamics. In this thesis, I aimed to determine if fruit from an invasive weed (barberry) influenced the behaviour of an endemic disperser (bellbird; Chapter 2). My results suggest it did not. Since the endemic disperser was not feeding on the fruit of the invasive plant, the next part of my study (Chapter 3) was designed to find out which bird species were. Three main and one minor seed dispersal vectors were observed removing fruit. Many of these birds were also observed feeding on a range of other fruiting species including native and introduced plants. Therefore, in Chapter 4 my objective was to determine the overall seed dispersal patterns of fruiting plants in Kowhai Bush. A range of dispersal mutualisms were observed between both native and introduced birds and native and naturalised plant species. In this chapter, the three previous research chapters will be discussed to highlight how findings from this thesis are important for current and future research.

5.1 Mutualisms

Janzen (1985) wrote: `Mutualisms have been thought to death; what we need are solid descriptions of how organisms actually interact, experiments with what happens when a potential mutualist is removed'. Bronstein (1994) stated that the opportunities to gaining new insights on mutualisms afforded by the movement of species to new habitats have been virtually ignored by biologists. Six years later Richardson et al. (2000) further stated that, given the increasing importance of alien plant invasions worldwide, and the important role that mutualisms play in facilitating these invasions, much more work is still urgently required.

As far as I know, the results in Chapter 2 are the first to quantitatively test if the removal of the fruit of an invasive alien plant affects the potential mutualisms with a native seed disperser. Initially, I suggested that the introduced weed, barberry, could be acting as a resource for endemic bellbirds and thus its removal could influence their behaviour. This was not the case as the bellbird did not feed on the exotic fruit and so its removal had little direct effect.

Despite this lack of interaction between bellbirds and barberry fruit, the effect of introduced fruiting vegetation on frugivores is a topic that has much potential in relation to understanding disperser mutualisms and the effects of invasive flesh-fruited plants on these mutualisms. Although no direct effects were observed in this study between bellbirds and barberry, this does not mean that other introduced fruiting plant species are unlikely to influence the behaviour of native frugivores. The three most important endemic frugivores in New Zealand have all been observed foraging on naturalised fruiting plants: bellbirds, *Cornus capitata* (Medway, 2009), *Arbutus unedo, Ilex aquifolium* and *Leycesteria formosa,* (Williams and Karl, 1996): kereru, *berberis darwinii* (Allen and Lee, 1992), *Cotoneaster* sp, *Crataegus* sp, *Ilex aquifolium, Ligustrum* sp, *Prunus* sp, *Psidium cattleyanum, Rosa eglanteria, Sorbus aucuparia,* (McEwen, 1978): and tui, *Leycesteria formosa* (Williams and Karl, 1996). It is possible that some of these foraging interactions are influencing the disperser's behaviour.

Frugivore – naturalized fruit mutualisms are not restricted to New Zealand. Carr (1993) reported that approximately 100 species, 8% of all naturalized flora in Victoria, Australia have fleshy fruit adapted for bird and mammal dispersal. A range of species in this area including emus (*Dromaius novaehollandiae*), silver gulls (*Chroicocephalus novaehollandiae*), black faced cuckoo shrikes (*Coracina novaehollandiae*), little wattlebirds (*Anthochaera chrysoptera*), red wattlebirds (*A. carunculata*), mistletoe birds (*Dicaeum hirundinaceum*), silvereyes (*Zosterops lateralis*), pied currawongs (*Strepera graculina*) and ravens (*Corvus coronoides*) have all been observed feeding on these naturalized species (Carr, 1993). Although fruit dispersal is primarily performed by birds in New Zealand, mammals and lizards are also important dispersers that should be considered within New Zealand and globally. In Victoria, Australia, kangaroos (*Macropus* spp), grey-headed flying foxes (*Pteropus poliocephalus*) and reptiles including cunningham's skink (*Egernia cunninghami*) have been observed feeding on the naturalised fruit species (Carr, 1993).

5.1.1 Pollination mutualisms in New Zealand

Although this thesis focused on seed dispersal mutualisms it is important to recognise that pollination mutualisms can also be affected by invasive flora. The impetus for carrying out the work in Chapter 2 was stimulated by a review by Bjerknes et al. (2007) on pollination mutualisms. Weedy species were observed affecting pollination regimes.

In this study, bellbirds earlier in the season were observed visiting barberry flowers (*pers. obs*.), so although barberry fruit did not influence the foraging behaviour of bellbirds, barberry flowering may have. There are more specialised pollination systems than specialised dispersal systems (Wheelwright and Orians, 1982). A review by Kelly et al. (2010) presents evidence for widespread pollen limitation in plants with ornithophilous flowers in New Zealand. It is therefore important to understand avian pollination dynamics and bird pollination in New Zealand.

5.1.2 Pollination and frugivory mutualisms

Pollination and seed dispersal go hand in hand (Regal, 1977, Jordano, 1987, Howe and Westley, 1986). Animals are often important transfer agents during both pollination of flowers and seed delivery to germination sites (Jordano, 1987). It is therefore important to observe mutualisms within both pollination and seed dispersal, to determine if invasive weeds are affecting avian foraging mutualisms in any form. Figure 5.1 shows the multiple pollination and dispersal interactions that could occur when a naturalised plant species becomes invasive in a new environment. These effects could be on the surrounding vegetation as a whole or on a single plant species, whereby a naturalised plant species might have a positive effect by drawing both pollinators and seed dispersers into an area. This in turn could increase pollination and dispersal of native vegetation in the surrounding vicinity of the naturalised plant species. Or a negative effect might occur instead where the naturalised plant species monopolises the pollinator and dispersers' time, reducing pollination and seed dispersal of the surrounding vegetation.

These possible mutualisms are important for conservation work. As observed with barberry, an invasive weed may not necessarily affect native disperser behaviour during the fruiting season but its subsequent removal could affect their foraging behaviour and subsequent pollination mutualisms during its flowering season. Thus both fruiting and flowering seasons should be considered when assessing if an invasive plant should to be subject to control or removed from an environment.

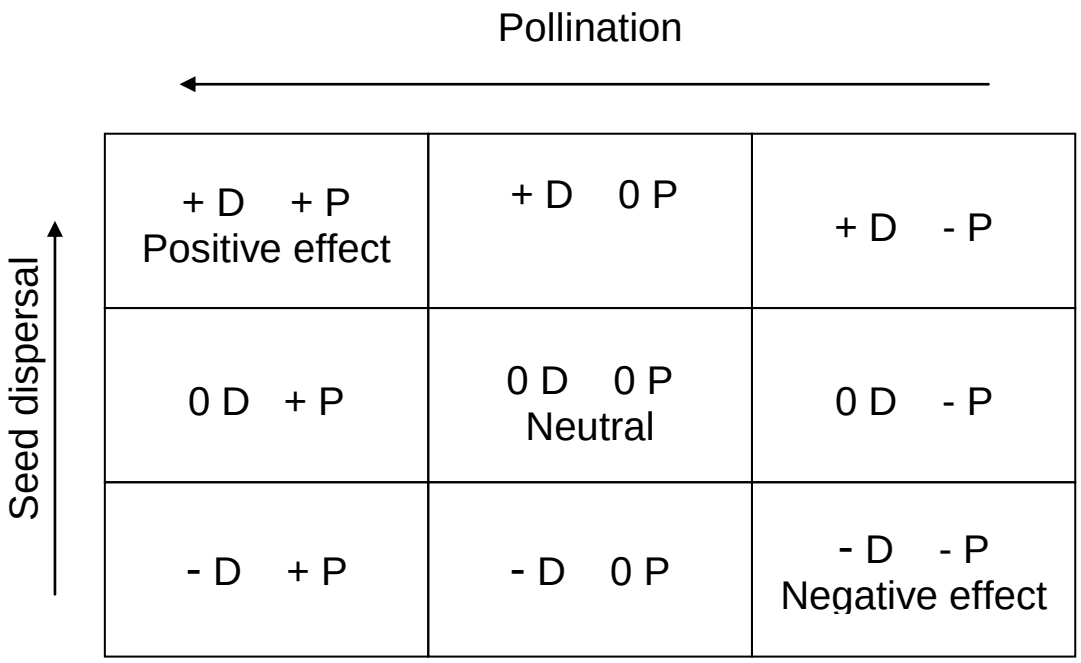

Figure 5.1. Possible effect an introduced plant species could have on pollination and seed dispersal mutualisms on surrounding vegetation. This table could be applied to a single plant species or within a forest. The arrows point to an increasing positive effect the introduced vegetation has on either pollination, represented as (P) or seed dispersal, represented as (D). Signs in the body of the table show the type of interaction (+, positive ; -, negative; 0, neutral).

5.2 Is the loss of disperser mutualisms important for fruiting plant invasions?

Richardson et al. (2000) noted in their review that the vast majority of cases involving seed dispersal mutualisms that resulted in the establishment of an alien plant species closely approximated associations that exist in the natural range of the introduced plants. An assessment of an introduced plant's opportunity for dispersal by birds is an important component for invasive plant screening procedures (Pheloung et al., 1999), as plant invasiveness is correlated with the number of dispersal agents (Stansbury and Vivian-Smith, 2003). Thus if a plant species retains dispersal mutualisms it is more likely to be invasive.

Yet it is unlikely that three introduced plant species from Europe, *Crataegus monogyna, Vitis vinifera* and *Taxus baccata* (Hill, 2011), in Kowhai Bush could have been dispersed by native seed dispersers alone as all three had fruit that was likely too large for native seed dispersers to easily swallow. Their dispersal could have been limited if it had not been for introduced blackbirds and song thrushes, which are also

native to Europe (Heather and Robertson, 1998), and are likely native dispersal vectors for these plants within their native ranges. It is possible that these three plant species were more likely to invade Kowhai Bush because they have not lost their dispersal mutualisms. This suggests that in particular situations the loss of dispersal mutualism could have had an important impact on the dispersal of plants as they enter a new environment.

5.3 Do introduced birds live up to their bad reputation in Kowhai Bush?

Traditionally, introduced frugivorous bird species have been portrayed in a poor light in New Zealand (Kelly et al., 2006, Williams and Karl, 1996). They are generally considered inferior dispersers for native vegetation and promote fleshy-fruited weed invasions throughout a number of native landscapes. The only introduced birds present in Kowhai Bush and considered major seed dispersers were blackbirds and song thrushes (Chapter 4). Although dunnocks and starlings were also observed feeding on fruit, this was rare and made it difficult to infer how important fruit was for these bird species. Given the results of my study, do introduced blackbirds and song thrushes deserve their poor reputation? The answer is both yes and no; there were a variety of reasons why they could be considered positive mutualists for native vegetation but there are also reasons why they were poor mutualists.

Blackbirds and especially song thrushes had positive aspects in relation to seed dispersal of native vegetation. Song thrushes had the second highest species richness in faecal samples. Furthermore, they were the only species observed dispersing native *Pseudowintera colorata* during this study. However, the major reason introduced blackbirds and song thrush could be considered positive influences in Kowhai Bush were through gape limitations. The two large endemic frugivores, tui and kereru, were largely absent from Kowhai Bush and therefore the dispersal of large seeds likely fell to blackbirds and song thrushes. Both introduced birds could swallow all of the fruit species in Kowhai Bush, which included native *Hedycarya arborea* and *Ripogonum scandens*. Native silvereyes and bellbirds were unlikely to feed on these species because of gape limitations. Although song thrushes and blackbirds were not observed in Kowhai Bush removing *Hedycarya arborea* and *Ripogonum scandens* they have been reported in the literature feeding on both (Clout and Hay, 1989).

On the other hand, both blackbirds and song thrushes did have negative aspects as fruit dispersers. Blackbirds were considered overall inferior dispersers for native vegetation in comparison to the other observed bird species. Both blackbirds and song

thrushes also dispersed adventive species at higher than expected rates in Kowhai Bush. This could facilitate the movement of invasive weeds through the native forest. Nevertheless, due to the limited numbers of observations collected for some of the bird species it is hard to evaluate how adequate or inadequate these introduced species were at dispersing seeds and maintaining ecosystem functioning within the native vegetation and more work is needed to determine if the positive effects outweigh the negative.

5.4 Invasional meltdown in Kowhai Bush and the creation of micro-environments by introduced frugivores.

Invasional meltdown is the process by which alien species facilitate one another (Simberloff, 2006, Simberloff and Von Holle, 1999). This is a community-level phenomenon in which the net effect of facilitations is an accelerated rate of establishment of introduced species and/or an increased impact (Simberloff, 2006, Simberloff and Von Holle, 1999). The role of alien-alien synergisms in facilitating invasions is commonly recognized and there are many examples where an established invader facilitates the establishment of later invaders not only through direct mutualisms but also through alteration of disturbance regimes or resource supply rates (Richardson et al., 2000). This applies to introduced frugivores and the dispersal of weeds.

Introduced birds were the only birds observed dispersing all of the introduced fruiting plants in Kowhai Bush at higher than expected rates. This in theory could create invasional meltdown through positive reciprocal benefits between the dispersers and fruiting plants. As the introduced fruiting species spread they will likely produce more resources for the introduced bird species, which further increases disperser populations and leads to increased dispersal rates of the invasive species (Fig. 5.2). The continuing expansion of introduced fruiting plants through Kowhai Bush by introduced birds would eventually change forest composition (Fig. 5.2).

Similar facilitative alien-alien synergisms involving frugivore dispersal of a weed species resulting in ecological damage have been observed nationally and globally. This has been observed with hawthorn *(Crataegus monogyna)* at Porters Pass, New Zealand. It was observed that as maturing hawthorn trees provided additional food and nesting sites for blackbirds, this subsequently led to increased dispersal of hawthorn and promoted its invasion into Porters Pass (Williams et al., 2010). Of the 90 major weeds in Hawaii, 33 (37%) are dispersed by predominantly alien, frugivorous birds (Simberloff and Von Holle, 1999). The fleshy-fruited tree, *Myrica faya,* in particular is

dispersed by introduced fugivores which have facilitated its spread through Hawaii's forests, which has disrupted native plant communities (Larosa et al., 1985). In Victoria, Australia, introduced blackbirds facilitated the spread of many serious environmental weeds including *Chrysanthemoides monilifera*, *Ligustrum lucidum*, *Myrsiphyllum asparagoides*, *Pyracantha coccinea* and *Schinus molle* through native forests (Carr, 1993). The red-whiskered bulbul (*Pycnonotus jocosus*) is a frugivorous invader that has disrupted plant communities in many habitats by acting as an efficient seed disperser for alien species such as *Rubus alceifolius* in La Réunion in the Mascarene Islands (Ian et al., 1991). Thus, it appears that a complex set of facilitative interactions among a variety of introduced species aids the invasion of weeds which are often detrimental to native forests, and this in turn can lead to alterations of native habitat composition.

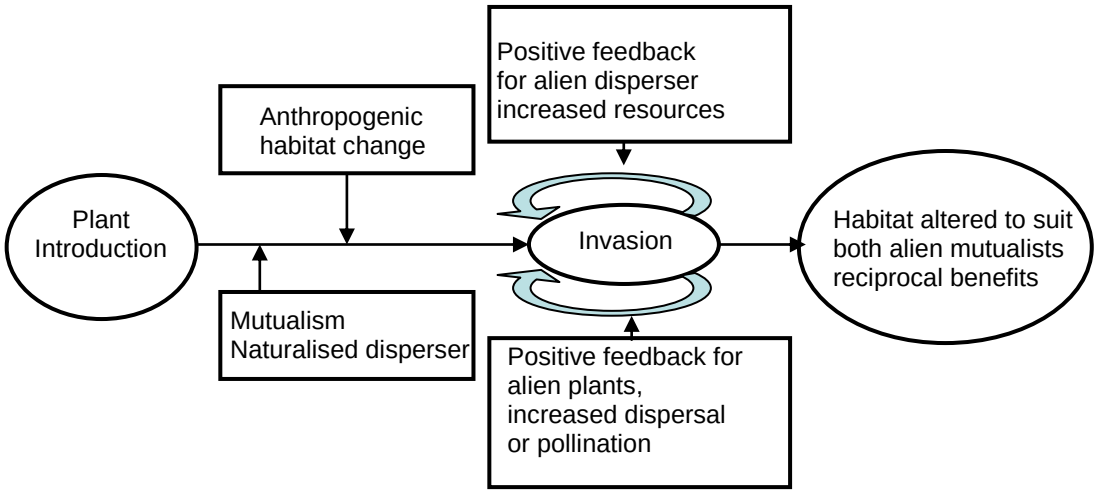

Figure 5.2. General model of invasion of alien plants facilitated by mutualisms (including pollination, seed dispersal and nutrient acquisition), and by anthropogenic changes to indigenous vegetation resulting in invasional meltdown. Note that successful invasions are often self-enforcing in that they further alter habitats and processes and benefit their own mutualists which results in the creation of micro-environments suited for both invasive mutualists. Figure based on Richardson et al. (2000) work.

5.5 Future research

Frugivore - plant interactions are common and are very important globally. There is much that can be learnt from these observations in relation to dispersal dynamics of both native and naturalised fruiting vegetation. The options for future research are numerous, but there are several key areas in which should be examined:

- How introduced plants influence both pollination and seed dispersal mutualisms in native forests.

- Understanding the roles introduced birds play in the movement of introduced plants through landscapes.

- How the loss or gain of dispersal mutualisms affects invasional success of plant species.

Despite the importance of plant-animal mutualisms, much of this field is poorly researched and inadequately understood. In particular, vertebrate pollination and dispersal regimes involving invasive plant species needs increased study. Similarly, the effects of introduced dispersers on dispersal systems needs both further descriptive work as well as experimental work that can demonstrate the breadth and extent of any novel mutualisms that have developed. This thesis has shown that the interactions among native and exotic fruit and frugivores are both complex, and important for the future composition of forest communities.

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